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Larvae—effect of parasitism on
Intercastes

Ants—host
Mermis—parasite

MERMIS PARASITISM AND INTERCASTES AMONG ANTS [1]

WILLIAM MORTON WHEELER

SEVENTEEN FIGURES

More than a quarter of a century ago (1901), I called attention to some singular structural and behavioristic modifications in a Texan ant, Pheidole commutata Mayr, as a result of infection by Nematode parasites of the genus Mermis. Several observers have since described similar phenomena in other species of Formicidae. In a very recent suggestive paper ('27), Vandel, after a study of some mermithized specimens of the Mediterranean Ph. pallidula Nyl., has rejected my early interpretation without noticing the change it has undergone in my subsequent publications ('07, '10, '26) and without a close study of my figures. For this reason and because I am able to give an account of several new cases of mermithism in certain Neotropical Formicidae, I have decided to review the whole subject. The discussion will show, I believe, that the effects of Mermis parasitism in ants are neither so easily interpreted nor so quickly disposed of as Vandel seems to imply.

HISTORICAL

Roger ('60–'61) was the first to notice peculiar, aberrant, microcephalic specimens of Odontomachus haematoda L., but he apparently regarded them as normal, undersized workers. In 1890, Emery, who encountered three of these individuals among material of O. haematoda from Costa Rica, tentatively described them as a new variety, 'microcephalus (?).' He

[1] Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, no. 286.

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likewise described a very similar specimen of O. chelifer
Latr. from Brazil as a new variety, 'leptocephalus (?).' In
the same paper he also noticed peculiar narrow-headed speci-
mens of Neoponera villosa Fabr. and Ectatomma tubercu-
latum Oliv. and two aberrant specimens of Pheidole absurda
Forel from Costa Rica. The latter, which he believed to be
ergatoid females, closely resemble the forms which I later
described ('01) as mermithized 'macroërgates' of Ph. com-
mutata. After the appearance of my paper, Emery reexam-
ined the various specimens mentioned in his contribution of
1890 and published an account of them in 1904. He found
Mermis in the abdomens of all the modified individuals and
also in single specimens of Pachycondyla fuscoatra Roger
from Bolivia and Paraponera clavata Fabr. from some lo-
cality in South America. The latter specimen, a worker,
showed no modification of the head, but merely a much
swollen gaster. I reproduce Emery's figures of most of the
forms which he studied (figs. 1, 2, 3, and 4).

In 1907, after finding a number of additional mermithized
individuals in two colonies of Ph. commutata, I published a
second account in my polymorphism paper. From this I
quote several paragraphs, because I propose to give in
another section of this article a more detailed description of
the specimens, which are still in my collection.

June 21, 1903. On revisiting New Braunfels (Texas) I found
on the very same hill slope two more colonies of Ph. commutata con-
taining mermithergates. On this occasion every effort was made
to secure the entire personnel of the colonies in a living condition.
One colony, confined in too small a bottle, died before I reached my
home; the other was successfully transferred to an artificial nest.
On examining the asphyxiated colony I found it to consist of many
female larvae and pupae, a few soldier and several worker larvae
and pupae, and a dozen mermithergates, which varied considerably in
size from individuals but little larger than the workers and without
ocelli, to huge individuals like those taken two years previously.
These large mermithergates possessed ocelli, a thoracic structure like
the soldiers and a rich red color like the females. Three pupal
mermithergates were also found but their gasters were not distended.
The earth of the nest contained two free Mermithes.

The personnel of the living colony comprised six adult and three pupal mermithergates, a winged and several pupal females, and a number of larval, pupal and adult workers and soldiers. All of the pupal mermithergates, like those in the asphyxiated colony, had the gaster in proper proportion to the remainder of the body, so that they appeared to be merely gigantic worker pupae. One of these hatched June 24, the two others July 2. As soon as they had hatched, their gasters began to enlarge rapidly and in the course of a few days the coils of the Mermis became visible through the distended pellucid membranes between the widely separated segmental sclerites. Evidently the parasites were present but of very small size in the pupae and grew very rapidly during the callow stages of their hosts while the chitinous investment of the gaster was still soft and distensible. This sudden growth of the parasite is probably due to the rich and abundant food with which the recently hatched callow is supplied by her sister workers.

This colony of Ph. commutata was kept under observation till August 12. Of the nine mermithergates which it contained, three had died by June 27, and three more by July 19, while the nest was being transported in my hand luggage from Texas to Colorado. Of the surviving three, two died July 25 and 30 and the last August 12. Hence at least one of these parasitized ants must have lived fully six weeks in the imaginal stage. In all of these cases the Mermis died within its host and both were carried to the refuse heap by the workers. One of the dead mermithergates had burst and the loops of the parasite protruded. In a state of nature it probably escapes from its host at this or an earlier stage, and enters the soil for the purpose of laying eggs. Or the eggs may, perhaps, be discharged into the alimentary tract of the ant and escape with its excrement. It is not difficult to conceive how they may find their way into the young larva. They may adhere to the body of the workers till gathered up by their strigils or tongues and transferred to the buccal pocket. Thence they could be fed inadvertently to the larvae, either with the regurgitated liquid food or with pieces of insects that had been malaxated and distributed by the workers.

The living mermithergates were easily studied in my artificial nest and exhibited several interesting peculiarities of behavior. On exposure to the sunlight they hurried, like the females, to the dark chamber, thereby evincing a much higher degree of negative phototropism than the workers and soldiers. They never carried the brood, although even the soldiers were seen to do this occasionally. They never fed the larvae, workers or females, and, had earth been present in the nest, it is very probable that they would never have shown any inclination to excavate. They never visited the manger

of the nest but were fed exclusively by regurgitation. As befitted animals containing such enormous parasites, they were in a chronic state of hunger. It was impossible at any time to uncover the nest without finding one or more of them either being fed by a worker or eagerly begging for food. And as soon as one was offered food, three or four of them would rush up and put out their tongues for a share of it. Once I saw a single worker trying to feed five of her huge parasitized sisters simultaneously. While imbibing their food the mermithergates stridulated, either continuously or at regular intervals. Sometimes they were so impatient to be fed that they would hold down a worker's head with their large fore feet and compel the little creature to regurgitate. Under these circumstances the larvae must have been poorly fed, for the insatiable mermithergates continually intercepted the workers on their way from the manger to the brood chamber. The mermithergates in my artificial nest may have been massacred by the workers and did not die merely as the result of parasitism for when the food supply becomes insufficient the tiny Ph. commutata workers, like those of Ph. instabilis, probably rid the colony of voracious and nonproductive mendicants, even when these belong to their own species. Apart from their chronic hunger, the mermithergates exhibited no abnormal traits of behavior directly attributable to parasitism. They ran about with as much alacrity as the workers and soldiers. Their other peculiarities, such as their strong negative phototropism, their dependence on regurgitated food, and the absence of the foraging instinct, like their large size, their ocelli and rich red color, may be regarded as female or soldier traits.

The supposition expressed in one of the preceding paragraphs in regard to the infection of the ant larvae by the Mermis through the alimentary tract may have to be abandoned, since various Mermithids are now known to enter their hosts by boring through the integument and to develop in the body cavity. Hagmeier ('12), who was the first to call attention to the inadequacy of my interpretation, succeeded in infecting young Locustids (Decticus), caterpillars (Smerinthus tiliae), and slugs (Limax agrestis) with larvae of Mermis albicans and concluded that they must enter their insect hosts by piercing their integument in the intersegmental regions. More recently, Cobb, Steiner, and Christie ('23) have actually witnessed the entrance of larval Agamermis decaudata into young grasshoppers.

On entering the host the driving mechanism is shed at a pre-determined, elaborately prepared node, and only the cephalic portion becomes parasitic. The node at which this automatic amputation takes place is prominent in the free-living larva. Persisting as a little altered terminal scar, it indicates that no moult occurs during the parasitic life. Usually the driving mechanism is left outside the host, but young larvae in which the node is unripe may take the driving mechanism inside, where, in the course of a few days, it is shed. The nema requires from two to five minutes to enter the host. This period is often preceded by a few minutes of waiting—perhaps devoted to some internal preparation for the onslaught. Entrance is bored at any thin part of the cuticle of the very young larva of the host—namely, on the head, thorax, abdomen or legs. . . . The entrance of the larva into its host, although very easily brought about in the laboratory, has not been observed in nature and doubt-less will be a matter very difficult of observation. The forecast is that the larvae will come to the surface of the ground in late spring, leave the soil, lurk among the decayed and living vegetation near the surface of the ground, and enter the host mostly at night.

That my original suggestion, however, was not absurd is shown by the fact that some nemas certainly enter the body cavity of the host by way of the alimentary tract. Hunger-ford ('19) thus describes the infection of the maggots of Sciara coprophila by Tetradonema plicans Cobb, a species resembling Mermis:

When young maggots not more than 3 mm. long were placed in earth containing the Nematode eggs, they would, in the course of a day or two, be found to contain sometimes as many as twenty-two young parasites. The parasite probably gains access to its host through the alimentary canal. Even newly hatched maggots are of sufficient size to consume solid objects larger than the egg of the nematode. ·The larger maggots habitually swallow bits of earth and solid pieces of organic matter many times the size of the eggs. As a matter of fact, I have found the eggs of this nematode in the digestive tract of small Sciara larvae, and believe that the young nemas hatching from eggs that have been swallowed, bore through the wall of the digestive tract into the body cavity of the maggot.

Cobb, Steiner, and Christie ('27) have recently observed that—

Mermis subnigrescens is found quite commonly in a number of varieties of common grasshoppers—for example the red-legged grasshopper Melanoplus femur-rubrum and its relatives. The hoppers become parasitized by swallowing eggs of the parasite that have been deposited on their food plants, these eggs containing well-developed young hairworms.

While artificially infecting the grasshoppers with M. subnigrescens, these authors made the important discovery that the sex of the parasites is determined by the number of them present in a single host. Summarizing their observations on this and other Mermithids they state that—

a high degree of parasitism resulted in the parasites being all males, or practically all; a very low degree of parasitism resulted in the parasites being all females. Between these extremes there was a gradient, with mixtures of males and females occurring, the proportion of males varying with the severity of the parasitism.[2]

In 1908, Mrázek discovered some mermithized virgin queens of the common European Lasius niger L. subsp. alienus Förster and called them 'mermithogynes.' These individuals closely resemble normal queens, except in having much shorter and smaller wings. In 1910, I described very similar specimens of L. niger var. neoniger Emery from Colorado, and, in 1921, Crawley and Baylis published an interesting study of Lasius mermithogynes observed in England and described the parasite as Mermis myrmecophila. They call attention to the fact that, as early as 1747, William Gould had seen this nema, which was subsequently named Gordius formicarum by Diesing (sine descriptione) in Lasius flavus De Geer. Crawley had observed Lasius mermithogynes in 1898 and had recorded them as 'brachypterous females' in 1910. In his and Baylis's paper of 1921 he gives a detailed description of them in Lasius niger alienus and flavus and shows from sections that, as a result of the parasitism, their fat-body is entirely consumed, that their ovaries are greatly

[2] These observations recall those of Malaquin ('01), who found that the sex of Monstrillid crustaceans, which are parasitic during their early ontogenetic stages in the blood vessels of marine annelids (Syllids), is determined in a similar manner.

reduced in size and have degenerating nurse cells, and that their tracheae tend to become hypertrophied. The behavior of L. niger mermithogynes in artificial nests is described as follows:

These mermithogynes were very active, often assisting callow ants to emerge from their cocoons, and were also very ravenous, devouring flies that I put into the nest, and also crippled and damaged pupae and callows, besides always asking the workers for food. Occasionally one would be seized with a kind of paralysis, lie on its back with legs and antennae extended and twitching, and a movement of the worm inside the gaster could be seen at the same time. Such ants usually recovered, but in one or two cases they died. After the emergence of the worms (by piercing the gaster near the posterior end) the ants became very active, but their death was only deferred a short time.

Donithorpe ('11, '15, '21, '26) has also described mermithogynes of the various species of Lasius above mentioned, and the lamented Professor Emery, in one of his last publications ('24), recorded two mermithogynes of L. umbratus Nyl. var. meridionalis Bondroit from Italy. Besides the diminution of the wings, these possessed a shorter, less quadrate, and anteriorly more narrowed head than the normal queen, and the antennal scapes, owing to the abbreviation of the head, extended farther beyond its occipital border. The scapes and tibiae lacked the erect hairs which were present in all the normal meridionalis queens which he examined. He notes that Crawley's figures ('21, figs. 1 and 3) of the mermithogynes of L. alienus and flavus also show a distinct narrowing of the head and thorax as compared with the unparasitized queen (fig. 2). Reexamination of seven of my mermithogynes of L. neoniger likewise reveals a perceptible decrease in the size of the head and a greater convexity of the posterior portion of the mesonotum.

Species of the genus Camponotus may also be mermithized. I described and figured a mermithergate of C. (Tanaemyrmex) pompejius Emery subsp. cassius Wheeler from the Belgian Congo. The specimen (fig. 6), except in the huge distention of the gaster, is in all respects like a normal worker minor. Its head shows no traces of ocelli.

Vandel's paper ('27) contains the most recent account of mermithized ants. He found at Miramont-de-Quercy, in southern France, a number of colonies of the small Pheidole pallidula containing infested individuals which he regards as being of the same structural type as my mermithergates of ˙Ph. commutata. Only two of these are represented in his figure which I reproduce (fig. 14). One of them (*a*) is obviously a microcephalic soldier, with the head much larger and the gaster much smaller than in any of the commutata mermithergates which I have described. The other specimen (*c*) is apparently a normal worker with an elongated gaster. He states that he failed to find ocelli in any of his mermithized specimens. On the basis of these observations, he rejects my thesis of 1901 that the mermithergates of Ph. commutata are enlarged individuals of the worker type, which owe their size to infestation by Mermis, but this thesis was clearly modified in my later papers in which I expressed the opinion that the mermithergates really exhibit mixtures of worker, soldier, and female characters, the form and size of the head being worker-like, the thorax and pedicel soldier-like, and the ocelli like those of the female. In my 'Sociétés d'Insectes" ('26, p. 249) I expressly stated that "dans les deux espèces de Pheidole (absurda et commutata) qui possèdant trois castes femelles bien nettement definies, reines, soldats à grosse tête et petites ouvrières, les mermithergates presentent un mélange singulier de leurs divers caractères." Vandel is scarcely justified, therefore, in contending (p. 39) that "il (Wheeler) s'en tient a son hypothèse de 1901, et il semble n'avoir changé d'opinion, dépuis lors."

Vandel also discusses the infection of the ants by the Mermis and its rate of growth. In regard to the infection, he asks:

At what moment does the parasite enter its host and how does it act upon it? We have had no information in regard to this matter up to the present time. Wheeler supposes that the parasite enters the larva of the ant, but this is a mere hypothesis. Now this is not the case—at least in the species which I have observed. I have, in fact,

never been able to find a Mermis in any stage of a Pheidole larva, either soldier or worker. In the prepupa of a soldier, however, I found a Mermis larva which certainly represents the stage of infection. This larva, in fact, is still furnished with the embryonic spine, which, as we know, disappears very soon after the beginning of parasitic life. This larva measures 450 μ in length and 36 μ in width. These observations show that the Mermis does not enter the Pheidole larva, but only the prepupa, at the moment of pupation.

I submit that, in my opinion, neither Vandel's inability to find Mermis larvae in the larvae of the Pheidole nor his finding a single young Mermis in a soldier prepupa constitutes satisfactory proof that the nema never enters the larvae, but only the prepupae of its host. And even if his contention is correct for Ph. pallidula, it can hardly apply to ponerine and formicine hosts, like Neoponera and Lasius, since the larvae in these subfamilies envelop themselves in tough cocoons before they reach the prepupal stage. We should have to suppose, therefore, on Vandel's assumption, that the Mermis waits till these tough envelopes have been spun and perforates them before entering the prepupae—a supposition which seems extremely improbable, since it must be so much easier to enter the naked, thin-skinned larvae. Almost certainly, also, the penetration by the Mermis, if delayed till the prepupal stage, would be too late to lead to such profound changes in the development of the imaginal head as I have described in Ph. commutata. But it is unnecessary to seek to refute Vandel with mere surmises. As a matter of fact, Hagmeier ('12, p. 527) not only found Mermis larvae in ant larvae, but was at least partially successful in bringing about the infection artificially. He specifically mentions (p. 529) finding young Mermis (presumably M. brevis Hagm.) in Myrmica rubra larvae in March, and this date indicates that the infected grubs must have been young.

Vandel's table of measurements of Mermis taken from ants in various advanced stages of development, from the unpigmented pupa to the imago, is interesting and confirms my observation (vide supra, p. 167) that the most rapid and conspicuous growth of the parasite occurs after the emergence

of the host. The nemas in white pupae with unpigmented eyes measured only 1 to 3.3 mm.; in those with pigmented eyes, 3.88 to 6.6 mm.; in yellow pupae, 8.3 to 14.4 mm.; in pale imagos (callows) 14 to 15 mm., and in the pigmented fully mature imagos 21 to 30 mm. The very slow growth of the larval Mermis, as shown in the table, suggests that it may enter,even very young larvae and take little food till the onset of pupation in the host. The single nema which Vandel found may therefore have entered the larva long before the prepupal stage. At any rate, we must conceive that the modifications in mermithized individuals are produced by the young parasite less than a millimeter in length, or only one-thirtieth of its adult dimensions, and that these modifications cannot be due to the withdrawal of considerable amounts of substance from the host's tissues, as I had supposed, but possibly to some toxic or inhibitory substance (enzyme?) secreted by the diminutive parasite. The fact that Vandel never succeeded in finding more than one Mermis in a worker or soldier of Ph. pallidula may explain why the modifications which he figures, and especially of the gaster, are so insignificant compared with those in Ph. commutata, which often harbor several nemas.

Recourse to the literature shows that Vandel was not the first to observe mermithergates in Ph. pallidula and that he has not described all the structural types which Mermis infection may induce in that ant. In 1909, Wasmann described and figured what he called "a remarkable, new, presumably parasitic ant," which was taken by Father W. Deckelmeyer near Barro, Portugal, in a colony of Ph. pallidula.

At first sight, says Wasmann, it resembles a transitional form between the soldier and worker of that ant. I describe it as Pheidole symbiotica. Only a few monomorphic workers were found, which probably—judging from their frontal ocellus and relatively voluminous gaster—are ergatoid females. The pupae sent from the Pheidole pallidula colony under consideration belong to this parasitic form; there was no queen of pallidula in the nest but only soldiers and workers. We may assume that we are dealing with a new parasitic ant, and with one in a very early stage of its origin.

When we compare Wasmann's detailed description and figure (reproduced as fig. 15) with Vandel's mermithergate (fig. 14, a) we see at once that the 'ergatoid female Ph. symbiotica' must be a mermithized specimen differing from Vandel's specimen only in having a smaller and more rounded head and in possessing a clearly developed median ocellus. Wasmann gives the length of his type specimen as 4 mm., with a body length equaling that of the soldier. In pilosity and the shape of the head it approaches the female pallidula, the antennae resemble those of the worker, and the thorax, though described as more slender, that of the soldier. This mermithergate, therefore, is very much like those of Ph. commutata, though the head seems to be larger. A year later (1910), Wasmann received all the remaining specimens of 'Ph. symbiotica' that had been retained by Father Deckelmeyer. They comprised four adults and one pupa of the 'ergatoid female' and six pupal males, which Wasmann regarded as the males of 'symbiotica,' so convinced was he that he had discovered a new parasitic ant. He then proceeded to describe the male from two pigmented pupae (!) and found that it differed slightly from the same sex in pallidula in having a more convex ocellar area, a more cylindrical first and longer terminal funicular joint.

The very questionable specific validity of 'Ph. symbiotica' did not escape Emery in his admirable revision of the Pheidoles of the megacephala group ('15). He easily disposes of the male with the remark:

I find similar characters (i.e., a cylindrical first and an elongated terminal funicular joint) in a male of the var. tristis and in a male (of the typical pallidula) from Portugal, taken with normal winged females; hence these males prove nothing in favor of Wasmann's thesis.

Concerning the 'ergatoid females,' he says:

The specimen figured by the author presents a striking resemblance to the individuals of Ph. absurda For., which I figured as ergatoid females but which have proved to be females or soldiers infested with Mermis. I communicated this supposition to Wasmann, who was

kind enough to clear one of his specimens in cedar oil in order to detect the convolutions of the suspected worm under the microscope. The result was completely negative; hence there was no Mermis in Ph. froggatti Forel

But this does not prove that the specimen had never been infected, since the Mermis may have escaped from its gaster, as in the mermithogynes described by Crawley (vide supra, p. 171) and in one of the Pheidole mermithergates to be described in the sequel (p. 193).

Since the foregoing historical paragraphs were written, M. Vandel has very generously sent me three of the Pheidole pallidula mermithergates which he took at Miramont-de-Quercy. They all contain Mermis, possess the anterior ocellus and head structure and are otherwise identical with Wasmann's 'Ph. symbiotica.' The consideration of these specimens in the sequel in connection with mermithized specimens of other species of Pheidole will show that Vandel's account requires some essential corrections.

MERMITHIZED PONERINAE

Emery, as we have seen, described several mermithergates in five large Neotropical ponerine ants, namely, Odontomachus haematoda (fig. 1), O. chelifer (fig. 2), Pachycondyla fuscoatra (fig. 3), Neoponera villosa inversa (fig. 4), and Paraponera clavata. All of these nest in the damp soil of the jungle floor, where conditions must be favorable for Mermis infection, except N. inversa. This savage stinging ant seems to be arboreal; at least, I have always found it, like the allied N. theresiae Forel, running up and down tree trunks, and all the nests I have seen of the typical villosa, which ranges from southern Texas to Brazil, were either in dead branches of living trees or about the roots of epiphytes.

Fig. 1 Odontomachus haematoda L. *a*, normal worker; *b*, head of same; *c*, mermithergate; *d* and *e*, heads of mermithergates; *f*, normal queen; *g*, head of same. (After C. Emery.)

Fig. 2 Odontomachus chelifer Latreille. *a*, head of small worker, with outline of head of large worker around it; *b*, mermithergate; *c*, head of same; *d*, head of queen. (After C. Emery.)
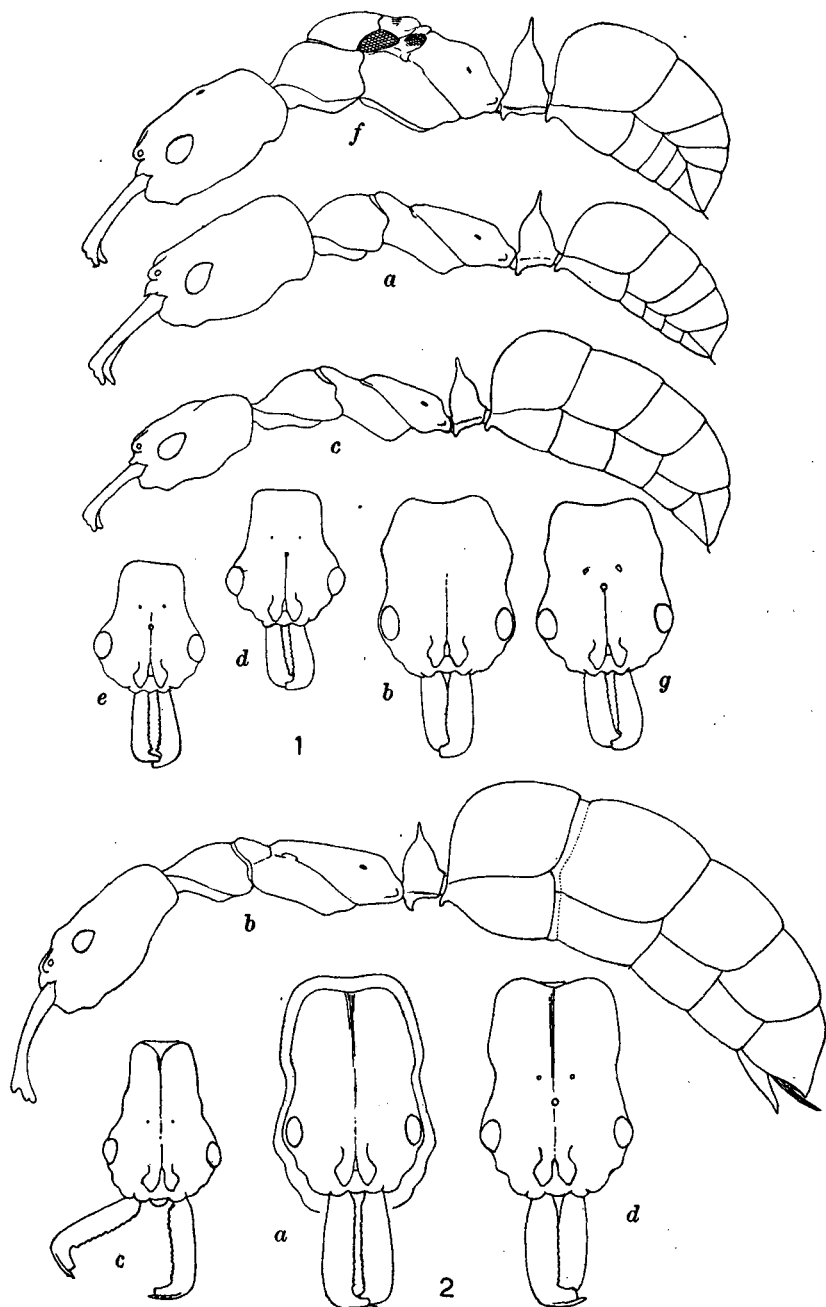
Figures 1 and 2

It is known also to nest in the pseudobulbs of large orchids (Schomburgkia).

In all his specimens, except Paraponera, Emery found the head considerably reduced in size (microcephalic) and of a peculiar narrow, rectangular shape behind the eyes. Small ocelli or ocellar pits were present in all the infested specimens of Odontomachus (figs. 1 and 2), but absent in the others. The thorax was in every case like that of the normal worker, the petiole in P. fuscoatra clearly like that of the queen (fig. 3). He concluded that—

the intensity of the effect of the parasite on the form of the body and especially of the head is not always the same: the degree of the modification depends on the proportion of the size of the worm to that of the ant. The greater the increase in the size of the worm and hence of the volume of the ant's gaster, the greater the modification of the head. Pheidole, therefore, shows the greatest change, then follow the two species of Odontomachus and Pachycondyla fuscoatra, then Neoponera inversa and finally Paraponera: In this huge ant the swelling of the gaster no longer exerts any effect on the form of the head.

But this interpretation is doubtful, since the parasites, if we may judge from the conditions in Pheidole, must be still very small in the pupae of the host and therefore at a time when the size and form of the head are already completely determined. It is more probable that the degree of modification of the host depends on the number of Mermis present in the larva.

The only ponerine mermithergate I have been able to examine is a well-preserved Neoponera inversa received from Dr. F. M. Gaige, who captured it in the Santa Marta Mountains, Colombia, July 21, 1913. He sent with it a large normal female taken in the same locality July 3rd. The infested specimen (fig. 5) measures 14.8 mm. Its head is very similar to that of the specimen figured by Emery (fig. 4, a), being much narrowed behind the eyes, with straight posterior border, but there is a distinct swelling, or convexity, behind each eye and at each of the posterior corners and the surface between these two pairs of swellings is rather deeply and trans-
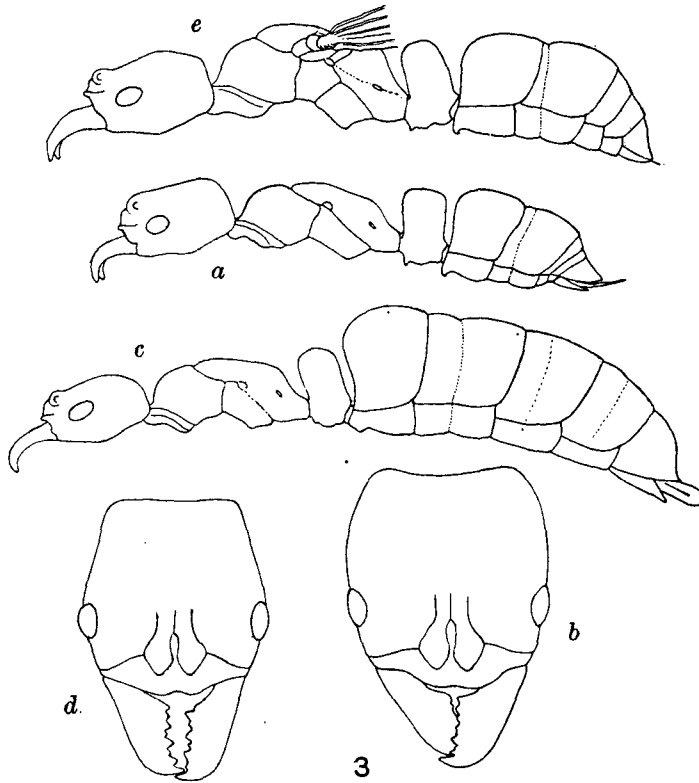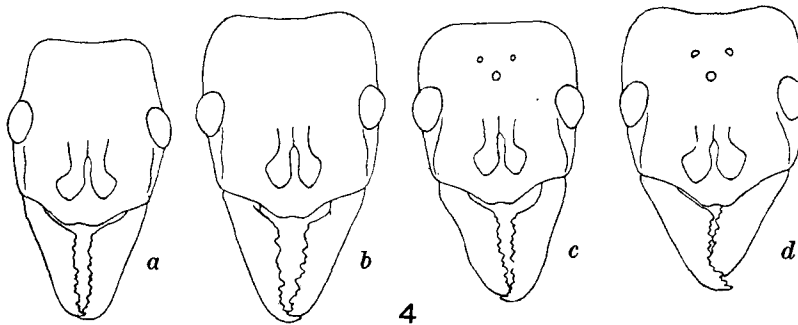
Fig. 3 Pachycondyla fuscoatra Roger. a, normal worker; b, head of same from above; c, mermithergate; d, head of same; e, normal queen. (After C. Emery.)

Fig. 4 Neoponera villosa F. Smith subsp. inversa F. Smith. a, head of mermithergate; b, of normal worker; c, head of queen (common form); d, head of queen from Venezuela. (After C. Emery.)

versely impressed on each side. There are no traces of ocelli.
The eyes are slightly larger and decidedly more convex and
protuberant than in the normal worker, though somewhat
smaller than in the queen. The antennal scapes are distinctly
less thickened toward their tips, and the mandibles are nar-
rower than in either of these castes. The thorax is longer than
in the worker, with longer pro- and epinotum, but otherwise of
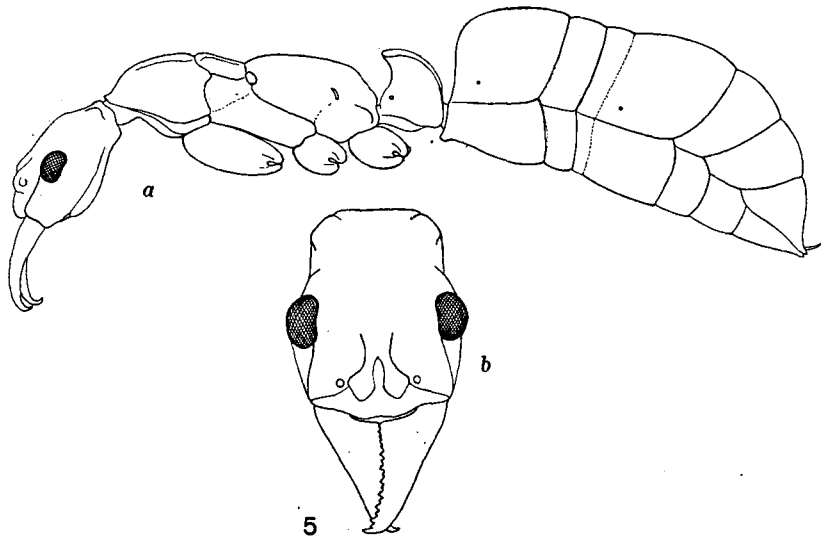the same structure. The petiole is shaped like that of the

Fig. 5   Neoponera villosa F. Smith subsp. inversa F. Smith.   a, mermithergate
in profile; b, head of same enlarged, from above.

queen, i.e., with the posterior surface round and convex and
not flattened above as in the worker. The gaster is much
swollen and even more voluminous than that of large queens.
Portions of the Mermis are visible through the integument,
which is thin and translucent in places. Owing to the finer
punctuation of the integument, the surface of the body and
especially of the mandibles is smoother and more shining than
in the worker and queen. In normal specimens of these castes
the hairs and appressed pubescence are golden yellow, but
in the mermithized specimen they are dull grayish; the

pubescence, however, is shorter, sparser, and finer, but the erect hairs on the body are like those of the queen, being longer, more delicate, and with more flexuous tips than in the worker.

According to Emery, there are two forms of normal queens in N. inversa, one of which (fig. 4, c) has a narrower head and more slender mandibles than the other (fig. 4, d). The normal worker (fig. 4, b) also has narrower mandibles than the large-headed queen. We might describe the mermithergate from Colombia as essentially a worker with queen abdomen and pilosity, but with a posteriorly much narrower head, more slender scales, smoother integument, and more feebly developed pubescence than in either of the normal female castes. Mermis infestation has therefore produced two sets of effects in this individual, one of which is a mixture of worker and queen characters, the other a departure from the normal characters of these two castes. In this connection we may also note the fact that several ponerine genera normally possess ergatoid queens which resemble the mermithergates in many particulars. This is true of Lobopelta, Onychomyrmex, Megaponera, Paranomopone, etc., in most species of which the only known queens have a wingless worker-like thorax, a somewhat higher, more gynaecoid petiole, a more voluminous gaster, and occasionally small, or vestigial ocelli. Such queens also occur in colonies of the common European and North American species of Ponera containing winged queens of the usual structure.

NOTES ON SOME LASIUS MERMITHOGYNES

Through the courtesy of Dr. A. H. Sturtevant, I am able to record some new observations on Lasius mermithogynes. During September, 1927, and also during the summer of 1926 he succeeded in finding a number of heavily mermithized colonies of Lasius niger var. americanus Emery nesting in the soil of old fields in three localities near Woods Hole and Falmouth, Massachusetts, and on Naushon Island. At my request, he generously sent me a lot of mermithogynes which

he collected September 30, 1927, at West Falmouth in three different nests, together with a number of normal winged queens, males, and workers belonging to the same colonies.

All of the mermithogynes, eighty in number, are remarkably uniform in stature and structure. The gasters of all of them are considerably distended with one or more coiled Mermithes, the largest of which measure 30 to 42 mm. Since Dr. N. A. Cobb, the eminent authority on the Nematodes, is studying the structure and development of these nemas at the Woods Hole Marine Biological Laboratory, I shall confine my remarks almost exclusively to the peculiarities of their hosts. In all of them the head and thorax are decidedly smaller than in normal queens of Lasius americanus; the head, excluding the mandibles, being as long or very nearly as long as broad and the antennal scapes extend in most specimens one-third their length beyond the occipital corners, whereas in unparasitized queens the head is distinctly broader than long, with the sides more convergent anteriorly and the antennal scapes extending little more than one-fourth their length beyond the occipital corners. The greatest differences, however, are discernible in the thorax, which in the mermithogynes is conspicuously smaller and less robust, narrower, and more suboblong, i.e., less subelliptical than in the uninfested queens, and much lower in profile. This is due to a very distinct depression of the mesonotum, which is only very feebly convex anteriorly and therefore but slightly higher than the raised posterior border of the pronotum. The mesosterna and mesopleura are also much less convex, but the epinotum is somewhat more prominent, so that it appears slightly longer when the thorax is viewed from above. These differences in the volume of the head and thorax of the mermithogynes in comparison with the corresponding regions in unparasitized Lasius americanus queens may be estimated from the following average measurements: The normal head is 1.7 mm. through the eyes and 1.4 mm. long, excluding the mandibles. The corresponding measurements for the mermithogynes are 1.3 mm. and 1.3 mm. In the unparasitized

queen the thorax is 4 mm. long, 2 mm. high through the mesosterna and scutellum, and 2 mm. broad through the mesosterna. The corresponding measurements for the mermithogynes are 2.7 mm., 1.4 mm., and 1.5 mm. The deficient development of the mesonotum and mesosterna is undoubtedly correlated with the small size of the vibratory muscles, and these in turn are correlated with the small size of the anterior wings, which are only 5.5 to 6 mm. long, though they measure 8.5 to 9 mm. in normal queens. The wing membranes of the mermithogynes are thicker, somewhat more opaque, and more densely pilose, and though the venation is normal, the veins are darker, more brownish and stouter even at their terminations, i.e., of more uniform thickness throughout. On this account, the venation seems to be coarser than in unparasitized queens. In nearly all the mermithogynes the dark brown tint of the head, thorax, and dorsal surface of the gaster is slightly paler and more reddish. I can detect no difference in the sculpture and pilosity of the body and appendages.

Doctor Sturtevant has also given me two mermithogynes of Lasius brevicornis Emery which he took from a colony at Falmouth, Massachusetts, September 25, 1927, nesting very near a mermithized colony of L. americanus. Both of these Lasii prefer to nest in rather dry, open grasslands, and it is not improbable that the Mermis which infested the brevicornis had spread from the americanus colony. The two mermithogynes are of the usual brachypterous type, their fore wings measuring only 5.7 mm., whereas those of normal brevicornis queen measure 8 to 8.6 mm. The head and thorax are very similar to those of the americanus mermithogynes in exhibiting a distinct diminution in size, though the head is clearly broader than long. The same peculiarities in the coloration and coarseness of the wing venation as in americanus are also observable.

The Mermithids, taken from the Lasius americanus females at Woods Hole are referred by Cobb, Steiner, and Christie ('27) to the genus Allomermis. They were able to establish

the fact that when a number of parasites in a single Lasius is large they are all or nearly all males, but that when the number is small they are females (p. 170).

POLYMORPHISM IN THE GENUS PHEIDOLE

The polymorphism, or poecilogyny of the female sex is feebly developed in the primitive ants of the subfamily Ponerinae compared with the more highly specialized species of the subfamilies Dorylinae, Myrmicinae, and Formicinae. And since Pheidole happens to be one of the myrmicine genera in which poecilogyny is most pronounced, it will be advisable to introduce some general remarks on its peculiarities before attempting to study the characters exhibited by the mermithized individuals. The difficulty in evaluating these characters is increased by the fact that Pheidole is a very large, cosmopolitan, though mainly tropical genus, comprising more than 400 species and more than 300 subspecies and varieties, many of which are based to a considerable extent on differences in body proportions due to polymorphism. And though the genus is in great part so homogeneous as to defy splitting into subgenera, it nevertheless contains a certain number of aberrant forms which must be taken into account in any general consideration of the development of the various castes.

The great majority of Pheidole species have three sharply defined female castes, workers (proper), soldiers, and fertile females (queens), which differ greatly in size and structure. The worker is small and slender, with well-proportioned body, small head, slender antennae and legs, denticulate mandibles of the usual type and short frontal carinae. Owing to its very close resemblance to the monomorphic workers of such genera as Aphaenogaster and Novomessor, it is very probably to be regarded as a more primitive or more ancient caste than the soldier. The body of the latter is shaped very much like that of the worker, though more robust, but the head is disproportionally and often excessively enlarged, subquadrate or subcordate, usually with a median

longitudinal groove and the posterior border more or less deeply emarginate, with well-developed frontal carinae, small and often flattened eyes, very convex mandibles, distinctly dentate only at the tip and base, and short antennae, with basally curved scapes. The queen is considerably larger than the soldier, very robust, but, owing to the voluminous, wing-bearing thorax and larger abdomen, of much more harmonious proportions. The head is large and broad, but shorter than in the soldier, with ocelli and large eyes, short antennae and mandibles of the soldier type. The three castes of the same species also differ more or less in sculpture, pilosity, and color. While the sculpture of the head in the soldier and queen is apt to be somewhat similar, it may differ greatly between the worker and soldier and in such a manner that it is impossible to predict from observation of the one what the other will be like. Thus in some species of Pheidole the head of the soldier may be heavily and peculiarly sculptured, while the worker has a smooth and shining head, and, conversely, the head of the worker may be opaque and densely punctate and rugulose, while that of the soldier is largely glabrous and shining.

The three female phases of Pheidole are obviously the result of differential growth (fig. 17). Apart from the wings and ocelli, which are confined to the fertile female, the four main regions of the body, i.e., the head, thorax, pedicel, and gaster, exhibit striking plus or minus developments of their various segments in the three castes. The soldier resembles the worker in its thorax and the queen in its head, while its pedicel is intermediate in form between those of the two extreme castes. The soldier's head, furthermore, exhibits so extreme an enlargement as to appear monstrous, or teratological, but it is clearly adaptive, since the great development of its width, length, and occipital lobes is correlated with the development of the mandibles and their adductor musculature (Wheeler, '27), and these in turn are adaptations to the granivorous, carnivorous, or omnivorous habits of the particular species. Emery ('21, p. 79) believed that the genus

Pheidole was originally granivorous and that the carnivorous
habit has been secondarily developed in some of the species,
but the reverse phylogenetic sequence seems to me to be far
more probable. In other words, the granivorous are probably
descended from carnivorous forms of Pheidole, just as the
granivorous species of Messor, Veromessor, and Novomessor
are descended from carnivorous Aphaenogaster-like forms.

Of the deviations within the genus Pheidole from the very
general scheme of polymorphism above outlined, attention
will be called to two only, those relating to the relative stature
of the three castes and those relating to the forms which in
certain species constitute transitions between the worker and
the soldier. In one minute and perhaps parasitic species (Ph.
microgyna sp. nov.), which I found in British Guiana, all
three of the castes are nearly of the same size. The fact
that the males of Pheidole are much smaller than the queens
and much more nearly of the size of the soldiers or workers
of their respective species indicates very clearly that the
fertile female caste was originally much smaller and more
like the other castes in size as in the Ponerinae and certain
species of Aphaenogaster and Stenamma. Hence if Ph. mi-
crogyna be really parasitic, the small stature of its queen is
probably due to a secondary reduction, but if it is non-para-
sitic, we may be dealing with a very primitive condition.

Some years ago ('15) Emery called attention to the fact
that in small, incipient colonies of Pheidole both the workers
and soldiers have smaller heads than in older, well-estab-
lished colonies, and that the soldiers of older colonies of the
same species in different localities may show considerable
variation in the size of the head as a result of climatic or
trophic influences. He is, therefore, no doubt correct in con-
jecturing that many of the described subspecies and varieties
of Pheidole have been based on such fluctuating, or phaeno-
typic variations. The differences in the size of the head of
the soldier in the various species of the megacephala group,
of which he has given a detailed account ('15), are of interest
in connection with the Ph. pallidula mermithergate described

by Vandel. Emery's figures (figs. 1 to 3) show that the smallest heads of the soldiers in this species, of its subsp. arenarum Ruzsky and of its var. reticeps Forel, are fully as small as in Vandel's specimen. The same is true of the allied Ph. jordanica Saulcy, as Emery has shown and as I find in a series of this ant collected in Palestine by Dr. W. M. Mann. Similar variations are also occasionally seen in some of our North American species, notably Ph. sitarches Wheeler, pilifera Roger, and vinelandica Forel. So far as its head is concerned, therefore, Vandel's mermithized specimen does not differ from the small-headed soldiers which normally occur in the colonies of pallidula and other Pheidoles. I shall return to this specimen in the sequel.

There is, however, another modification which is characteristic of certain Pheidoles belonging to various groups of species and to two allied genera, Machomyrma and Ceratopheidole. This is the normal occurrence of a series exhibiting more or less numerous intergrading forms in the size and sculpture of the head and thorax and the shape of the body between the usual microcephalic worker and the macrocephalic soldier of the same species. These conditions are therefore very similar to those observed in the allied genera Messor and Novomessor. The list given on page 188 is somewhat more complete than that given by Emery ('15) of the species of Pheidole and closely allied genera in which this peculiarity has been observed.

The forms listed in this table very probably represent more primitive conditions of the polymorphism of the original sterile worker caste than the more numerous species of Pheidole in which it is sharply differentiated into workers proper and soldiers. This is also indicated by the intergrading worker and soldier forms in other genera among the Myrmicinae, Dorylinae, Dolichoderinae, and Formicinae (Messor, Pheidologeton, Atta, Dorylus, Eciton, Azteca, Camponotus, etc.). The species enumerated in the table, however, differ among themselves in the completeness of their series of intergrades. Thus, in large colonies of Ph. kingi instabilis it is

possible to find a continuous series of annectant individuals
between the typical worker and the typical soldier, but in
Ph. rhea and to some extent also in Ph. vasliti, the inter-
grades nearest the soldier type are most numerous, and this is
so definitely the case in some colonies that two soldier castes,
represented, respectively, by larger- and smaller-headed in-
dividuals, may be distinguished. According to Emery, simi-
lar conditions obtain in Ph. reddenburgensis and capensis,
the former exhibiting a complete series of intergrades, the

Ph. vasliti Pergande with var. hirtula Forel, var. acolhua Wheeler, subsp. subdentata Pergande and its var. arizonica Santschi Ph. rhea Wheeler with vars. sinaloana, catalina and gaia vars. nov.	Group Fallax—Southern United States and Mexico
Ph. kingi Ern. André with subsp. insipida Forel, instabilis Emery and torpescens Wheeler Ph. tepicana Perg. with subsp. calens Forel and cavigenis Wheeler Ph. macclendoni Wheeler Ph. centeotl Wheeler	Group Subarmata— Southern United States and Mexico
Ph. cuitensis Forel Ph. capensis Mayr and its subsp. reddenburgensis Forel	Group Megacephala— Africa
Ph. froggatti Forel	Subgenus Isopheidole Emery—Australia

Machomyrma dispar Forel and silvestrii Emery...................Australia

Ceratopheidole smythiesi Forel................................Indomalaya

latter a gap between the workers and small-headed soldiers.
So much can be gleaned from the series of specimens ordi-
narily selected to represent the various species in our cabi-
nets, but the collection of much more extensive series or the
whole personnel of colonies, their careful measurement and
statistical treatment will have to be undertaken before we
shall be able to make more precise statements. We are in
great need of such very special studies not only in the genus
Pheidole, but also in many other genera, e.g., Eciton, Atta,
Messor, Solenopsis, Azteca, Camponotus, etc.

For reasons to be given later, I propose to call the various annectant forms between the extreme castes of the same sex in ants and other social insects 'intercastes,' to distinguish them from the 'intersexes,' which constitute normal or pathological intergrades between the sexes. Intercastes occur also between different castes of fertile females in ants, e.g., between ergatoid and winged queens and between workers and
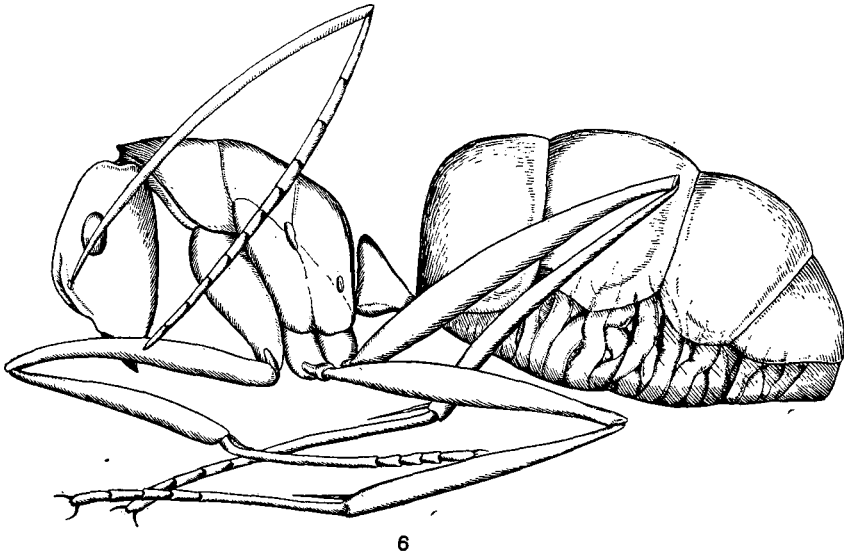

Fig. 6 Mermithergate of Camponotus (Tanaemyrmex) pompejus Emery subsp. cassius Wheeler.

queens (Leptothorax, Formicoxenus, Monomorium, Myrmecina, Crematogaster, Polyergus, etc.).

MERMITHERGATES OF PHEIDOLE

Although mermithergates seem to occur more frequently in species of Pheidole than in any other ant genus, it must not be supposed that these anomalies are common. During the past thirty years, I have collected a great many Pheidoles in many localities, but have succeeded in finding only a few mermithized colonies, and these belonged to only two species,

Ph. commutata and gouldi. Vandel informs me that infested colonies of Ph. pallidula seem to be very local in southern France, but in his paper ('27, p. 41, nota) he says:

The parasitized nests are frequent in the region which I explored, and though I have kept no precise records, it seems to me that nearly half of the nests I examined contained mermithergates. As a rule the mermithergates in each nest are few in number, but sometimes the parasitism becomes intense. Thus in one very small nest I was able to count 22 adult mermithergates.

The fact that the colonies I have observed in the field were all nesting in rather damp, shady spots leads me to believe that the various species of Mermis which infest ants must require for their adult development either a peculiar kind of soil or certain conditions of humidity which are commonly shunned by the species of Pheidole. For the most part the species of this huge genus prefer rather dry, open, sunny country. Their colonies are few and sporadic in damp forests even in the tropics.

Of the six species of Pheidole enumerated below, I have been able to examine mermithergates of five.

1. *Pheidole gouldi Forel* (*biconstricta group*) (fig. 7)

This species was originally described by Forel from females, soldiers, workers, and males taken by Stoll at Antigua, Guatemala. I have also taken it both in the type locality and also at Escuintla in the same republic. In one of the colonies in the latter locality I found a single mermithergate on the last day of 1911. I have not seen the queen of the typical gouldi, but have used for comparison a fine series containing queens of a larger and more reddish subspecies (tonolana subsp. nov.) taken by Prof. A. Petrunkevitch at Tonola, in Chiapas, Mexico.

The mermithergate from Escuintla (fig. 7, *a*) measures 6.2 mm. It is somewhat larger than the soldier, which is somewhat less than 6 mm., and nearly twice as long as the worker, which measures only 3.3 to 3.5 mm. It resembles the worker

in form, but the gaster is enormously distended with Mermis, the head (fig. 7, *b*) is broader behind, with a shorter occipital collar, and its color is much paler and more reddish. There are no traces of ocelli. The thorax and pedicel are shaped and sculptured as in the soldier (fig. 7, *d*), i.e., the pronotum and epinotum are transversely rugulose above, but the pro-
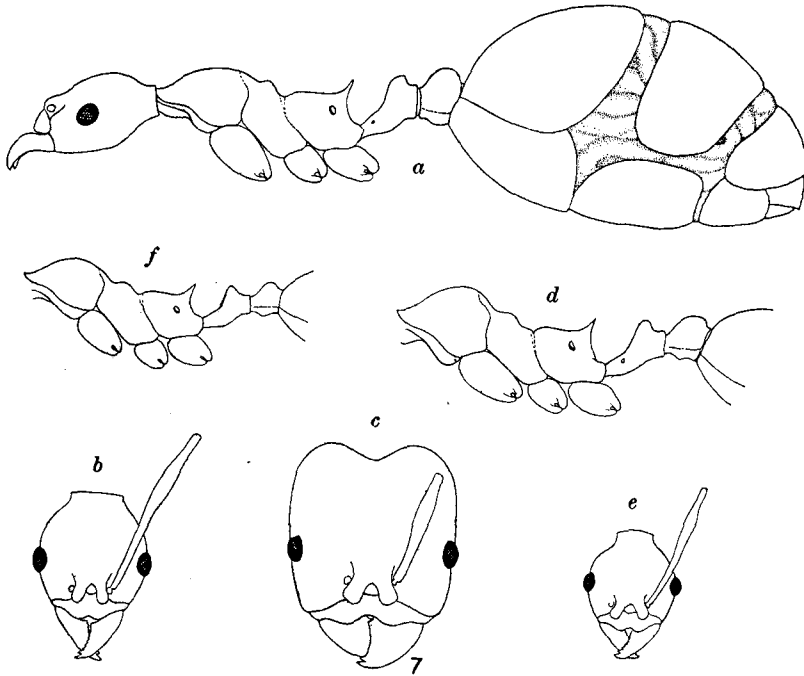

Fig. 7 Pheidole gouldi Forel; *a*, mermithergate; *b*, head of same; *c*, head of soldier; *d*, thorax and pedicel of same; *e*, head of worker; *f*, thorax and pedicel of same.

notum is less convex in profile and more like that of the worker (fig. 7, *f*) in shape. The gastric sclerites are enlarged as in the soldier, but the legs and especially the antennae are decidedly longer and more slender and therefore of the worker type. The erect hairs on the body and appendages, however, are longer and more numerous as in the soldier. I can detect no distinct resemblances to the queen in this mermithergate.

2. *Pheidole opaca Mayr var. near incrustata Forel* (*biconstricta group*) (fig. 8)

A single well-preserved mermithergate labeled 'Guatemala,' and accompanied by a normal worker of a form intermediate between the typical opaca and Forel's var. incrustata,
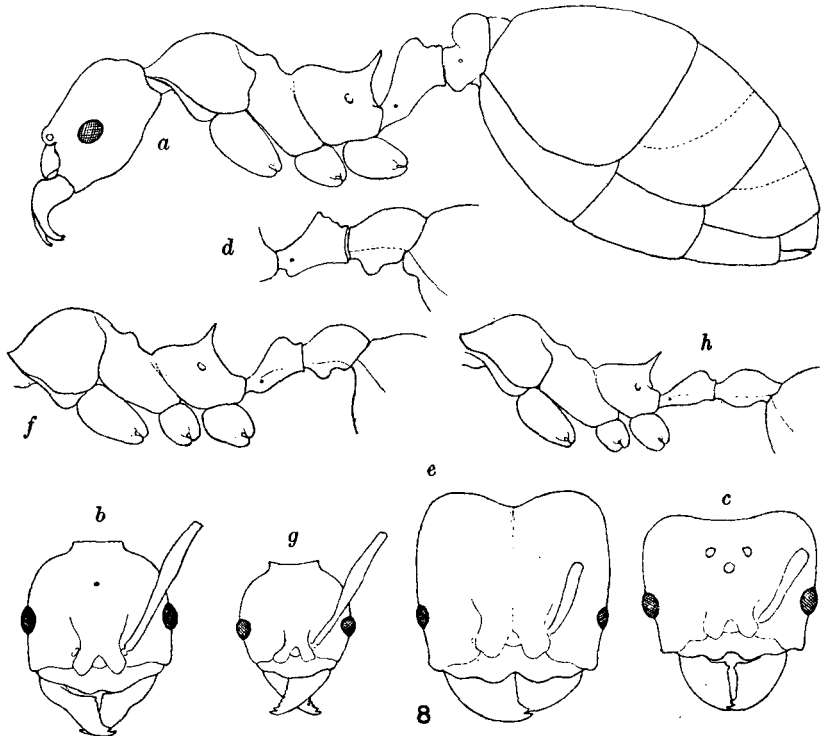

Fig. 8   Pheidole opaca Mayr. var. near incrustata Forel; *a*, mermithergate; *b*, head of same; *c*, head of queen Ph. opaca (typical); *d*, pedicel of same in profile; *e*, head of soldier of Ph. opaca var. incrusta; *f*, thorax and pedicel of same; *g*, head of worker; *h*, thorax and pedicel of same.

originally described from specimens taken by Pittier at Tuis, Costa Rica, came to me among some ants belonging to the Pergande collection. The two specimens have been compared with queens, soldiers, and workers of the typical opaca from various South American localities (British Guiana, Mexiana Island, Pará, and Rio Madeira, Brazil). The mermithergate

(fig. 8, *a*) measures 6.5 mm. (the soldier of the typical opaca is nearly 7 mm.) and has the gaster greatly distended, but empty and translucent, the Mermis having escaped. The head (fig. 8, *b*) is very different from that of the worker (*g*), being larger, broader in front than behind, with short but distinct occipital collar. The mandibles are aberrant in having the external borders decidedly concave in the middle; the clypeus is carinate, with its anterior border distinctly sinuate in the middle as in the soldier (*e*) and queen (*c*) (entire and non-carinate in the worker); the frontal carinae are long and pronounced, the ocelli absent, but there is a distinct anterior ocellar pit. In coloration the head and mandibles are worker-like, but the sculpture of the head and thorax is even coarser than in the soldier of the typical opaca; the front and sides of the head are strongly longitudinally reticulate-rugose. In shape the thorax and petiole are much like those of the soldier, but the postpetiole differs from that of any of the castes, though it is most like that of the queen (*d*). Seen from above, it is nearly three times as broad as long. The legs and antennae are of the worker type.

3. Pheidole susannae Forel subsp. atricolor Forel (biconstricta group) (fig. 9)

Dr. George Salt recently sent me part of a colony of this ant taken November 21, 1926, at Rio Frio, Colombia, and consisting of numerous larval, pupal, and adult workers and soldiers and three adult mermithergates. I have not seen the queen of this subspecies, but have compared the specimens collected by Doctor Salt with series of the typical susannae from Guatemala, the subsp. obscurior Forel from the Island of St. Vincent and British Guiana, the var. fortunata Forel from Costa Rica, and the allied species Ph. grallipes Wheeler from Southern California and Ph. longiscapa Forel from Venezuela. The normal soldier of atricolor measures 3.4 to 3.8 mm., the normal worker 2.5 to 2.8 mm. The latter, like the workers of the other subspecies and varieties of susannae

and of the allied species, is peculiar in having an elongated elliptical head (fig. 9, e), constricted posteriorly to form a
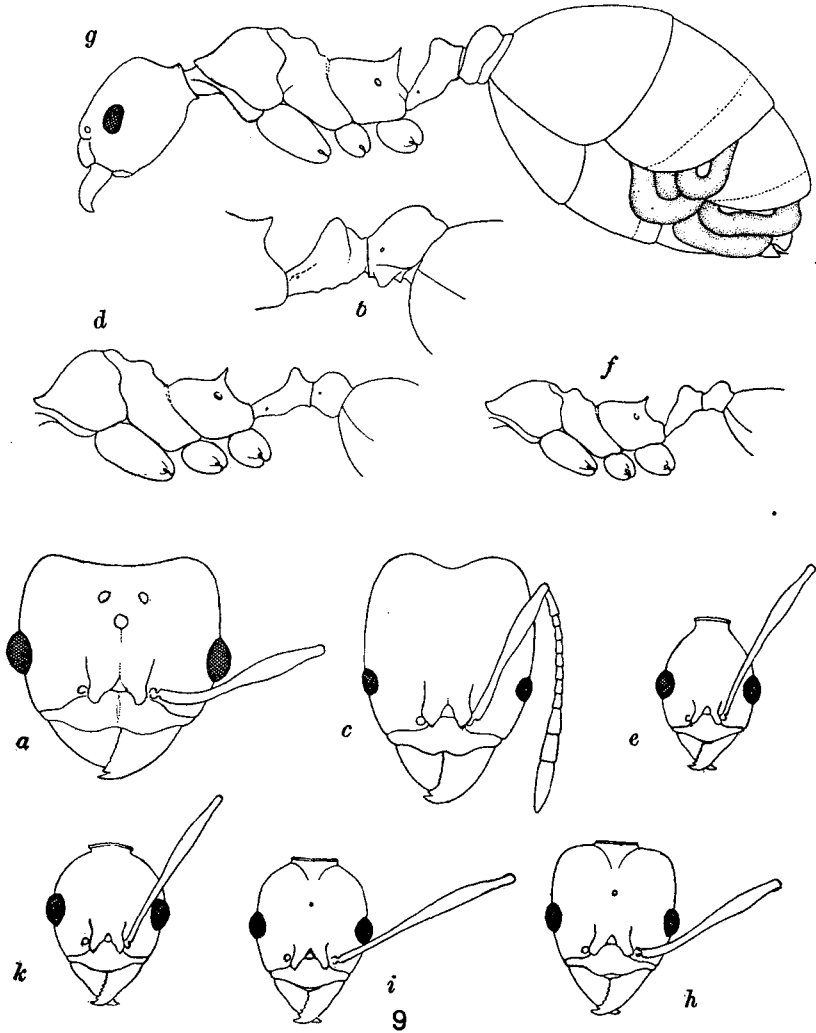

Fig. 9 a, head of queen of Pheidole susannae Forel var. near subsp. obscurior Forel; b, pedicel of same in profile; c, Ph. susannae subsp. atricolor Forel, head of soldier; d, thorax and pedicel of same; e, head of worker; f, thorax and pedicel of same; g, mermithergate (A); h, head of same; i, head of mermithergate (B); k, head of mermithergate (C).

neck with a distinct occipital collar. The three mermither-
gates measure 4 to 4.5 mm. and have the gaster greatly dis-
tended with Mermis, but they differ from one another in
certain details of structure and sculpture, so that it will be
best to describe them separately as (A), (B), and (C).

(A) measures 4.5 mm. (fig. 9, *g*). Its head (fig. 9, *h*) is
decidedly larger than that of the worker and of a very differ-
ent shape, being subrectangular, nearly as broad as long,
with distinct, short, narrow, abrupt occipital collar and a flat,
shining anterior ocellus, but no traces of posterior ocelli.
The antennae are slightly shorter than in the worker, with
the base of the scapes more thickened and curved as in the
soldier. The eyes, however, are convex like those of the
worker. The mandibles, though of a similar shape, are more
robust. The clypeus is convex as in the worker, but its an-
terior border is distinctly emarginate in the middle as in the
soldier and queen. The thorax and pedicel (fig. 9, *g*) are
soldier-like, but more robust, especially the pedicel, and the
postpetiole is much larger and broader and therefore more
like that of the queen (*b*). The gastric segments are enlarged
as in the soldier and queen, but the legs are long like those
of the soldier and worker. The sculpture is peculiar, the
body being entirely opaque and densely and coarsely punc-
tate, except the mandibles, clypeus, and legs, which are
smoother and shining. The normal worker is shining, with
only the meso- and epinotum and the anterior and ventral
portions of the petiole subopaque and densely punctate. In
the soldier the head is longitudinally punctate and rugulose,
except the posterior corners, which are smooth and shining.
The thorax is somewhat less opaque than in (A), the pro-
notum somewhat shining and transversely rugulose above,
the gaster shining and finely punctate, with only the anterior
portion of the first segment subopaque. In color (A) is very
dark, being black, with only the mandibles, antennae, and
articulations of the appendages reddish brown and the tarsi
paler and more yellowish. The pale pilosity on the body
and appendages is quite as long and abundant as in the soldier
and much more abundant than in the worker.

(B) is of the same size as (A) and the head (fig. 9, *i*) is of the same general shape, but smaller and narrower, and with more rounded posterior corners. There is a small anterior ocellus and a trace of the occipital groove as in (A); the antennae are long and like those of the worker and the anterior clypeal border is entire. The legs are somewhat more slender, as in the worker. The thorax and pedicel are very soldier-like, but the postpetiole, as in (A), is larger and more like that of the queen. The sculpture resembles that of the soldier, the head and gaster being much more shining than in (A). The head is longitudinally rugose even to the occipital collar, and its posterior portion has the shallow, oblique foveolae of the soldier. The color and pilosity are also like those of the latter caste.

(C) measures only 4 mm. Its head (fig. 9, *k*) is smaller than in (B) and more like that of the worker, without posterior corners, but scarcely constricted behind. There are no traces of ocelli or of ocellar pits. In other respects the specimen is much like (B), but the postpetiole is smaller and more like that of the soldier.

It is obvious that these mermithergates represent three different degrees of departure from the worker type. In (B) and (C) the head is more nearly worker-like in form, whereas in (A) it distinctly approaches the queen, both in shape and sculpture. Although I have not seen the queen atricolor, the queens of the very similar subspecies obscurior and of the allied Ph. grallipes show that this caste must have the exposed portions of the gastric sclerites opaque and densely punctate and therefore quite unlike the normal gastric sculpture of the soldiers and workers. The broad postpetiole and large gastric sclerites of (A) and (B) are also clearly queen characters. All three mermithergates of atricolor, therefore, show a distinct intermingling of the three female castes with predominance of the worker and of the queen in (A) and (B) in the head, of the soldier in the thoracic, and of the queen in the abdominal, region.

4. Pheidole commutata Mayr (fabricator group) (fig. 10)

The head of the normal worker of this species (fig. 10, *e*), though narrowed posteriorly, is very different from that of susannae, since it possesses no neck-like constriction nor oc-
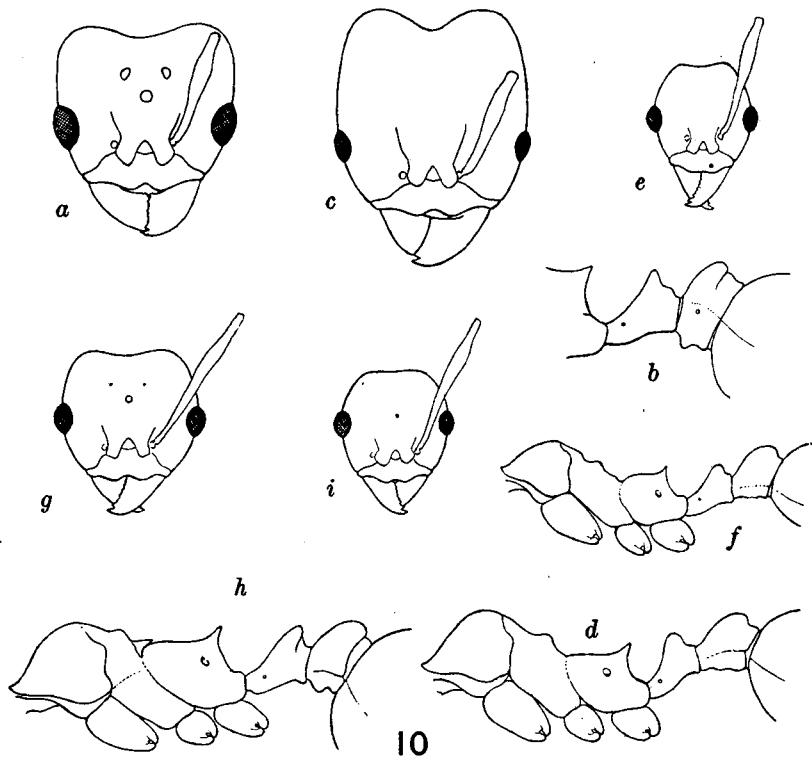

Fig. 10   Pheidole commutata Mayr. *a*, head of queen; *b*, pedicel of same in profile; *c*, head of soldier; *d*, thorax and pedicel of same in profile; *e*, head of worker; *f*, thorax and pedicel of same in profile; *g*, head of mermithergate (A); *h*, thorax and pedicel of same in profile; *i*, head of mermithergate (B).

cipital collar.   On reexamination, the dozen mermithergates which I placed in my collection in 1903 prove to be separable into three series corresponding to the three specimens (A), (B), and (C) of Ph. atricolor above described.   All of them have the gaster greatly distended with Mermis.

Series (A) is represented by seven specimens which measure 4 to 4.5 mm. and have a head of the form shown in figure 10, *g*. The anterior ocellus is distinct in all of them, and there are either minute posterior ocelli or small ocellar pits. The head somewhat resembles that of the soldier, but may be more accurately described as combining the characters of the queen and worker (fig. 10, *a* and *e*), since the antennae are long and of the worker type and small ocelli are present. Some of the specimens have the clypeus distinctly notched, while in others it is nearly entire. The thorax and petiole are soldier-like, but several specimens (fig. 10, *h*) have a small but distinct scutellar sclerite, which is an approach to the conditions in the queen. The postpetiole, too, is more as in that caste. The sculpture of the head, though smoother and more shining, approaches that of the queen, the longitudinal rugae extending much farther posteriorly than in the soldier. The pilosity is long and bristly like that of the latter caste, but the color in several specimens is much more reddish and therefore more like that of the queen.

Series (B) comprises two specimens, measuring 3.5 mm., with smaller and narrower head (fig. 10, *i*) and therefore more like the worker. The anterior ocellus is represented by a minute pit. The specimens also approach the worker in the sculpture of the head, which is smoother and more shining, and in the shape of the pronotum, which is lower and less convex than in the soldier; the remainder of the thorax and the pedicel are like the corresponding regions in the soldier, and the pilosity is abundant and bristly as in that caste.

Series (C) comprises three specimens measuring only 3 mm. They are quite like the normal worker, which measures 2.3 to 2.6 mm., except that the postpetiole is decidedly larger and broader, the pilosity slightly more abundant and the gaster swollen with Mermis.

5. Pheidole absurda Forel (praeusta group)

I reproduce Emery's figures of 1890 (fig. 11) and 1904 (fig. 12) of his two mermithergates of this Central American ant. In the later figure (fig. 12, b) the ocelli are omitted, apparently as an oversight. Emery interpreted the specimens as 'microcephalic soldiers' rather than as 'parasitically castrated, microcephalic females,' but the ocelli are a queen character and the mandibles and antennae are clearly worker- and not soldier-like. The shape of the head, however, resembles that of the soldier, and not that of the worker (f) or queen, unless the future discovery of this caste shows it to have an elongate head, broader anteriorly than posteriorly, and this is very improbable, judging from the many species of Pheidole of which the queen is known. Comparison of Emery's figures with those of all the Pheidole mermithergates above considered reveals a very similar mingling of the peculiarities of all three castes, the head having worker, soldier, and queen, the thorax soldier, and the pedicel and gaster female characters.

6. Pheidole pallidula Nylander (megacephala group)
(figs. 13 to 15)

In his account of the mermithergates of this species found at Miramont-le-Quercy, Vandel ('27) describes two types. One of them (fig. 14, e) has the stature of the ordinary worker (g) and is unmodified. His figures show that the only difference is in the elongation of the Mermis-containing gaster of the former, though the first segment is significantly enlarged. The other type (fig. 14, a) is obviously a small-headed soldier with certain worker and female characters and is described as follows:

Comparative morphological examination of the mermithergate and the soldier discloses their affinities. The stature is the same in both cases (3–4 mm.). The abdomen is swollen and more elongate in the mermithergate than in the soldier, but this is due simply to the distention provoked by the parasite. In size and shape the mandibles

are intermediate between those of the soldier and the worker. The mandibles of the soldier are almost devoid of denticles (fig. 14, d) but there are a few denticles on the mandibles of the soldier (b) ; on those of the worker (f) they are numerous and well-developed.

The principal differences are in the form and dimensions of the head. Instead of the enormous head of the soldier, the length of which represents more than a third of the total length of the animal, the mermithergate has a small head, scarcely more than a fifth of the total length. The sides of the head are arcuate in the mermithergate as in the worker, whereas they are parallel in the soldier. The head is concave posteriorly as in the soldier but much more feebly. It exhibits a trace of the median impression which is so marked in the soldier though completely absent in the worker. Finally, the head of the mermithergate is ornamented with coarse longitudinal rugae, whereas that of the worker is almost smooth.

Morphological study therefore leads us to maintain that the mermithergate does not represent an hypertrophied worker but a modified and degenerate soldier and that the action of the parasite is confined principally to the head. Far from having undergone, as Wheeler would have us believe, an exceptional growth, the mermithergate exhibits obvious signs of reduction, like most animals modified by parasitism.

The study of their behavior confirms the same conclusion. The soldiers are extremely courageous and, when the nest is disturbed, they are seen to run about in all directions with wide open mandibles, endeavoring to grasp any object within reach and particularly the tweezers with which one attempts to seize them. The behavior of the mermithergate is very different, as Wheeler has already remarked ('07, p. 22). They are timorous creatures which are found lurking in the darkest corners, among the masses of brood, and flee when an attempt is made to capture them. It is worthy of note that the disappearance of the combative instinct is correlated with a loss of the organ of attack (namely, the mandibles which are worked by the powerful muscles that fill out a large portion of the enormous cranium of the soldier). This example shows once more that function and organ are two things indissolubly united and impossible to dissociate.

Fig. 11   Pheidole absurda Forel.   Mermithergate, with ocelli.   (After C. Emery.)

Fig. 12   Pheidole absurda Forel. a, soldier, in profile; b, head of same from above; c, worker; d, head of same; e, mermithergate in profile; f, same from above.   (After C. Emery.)
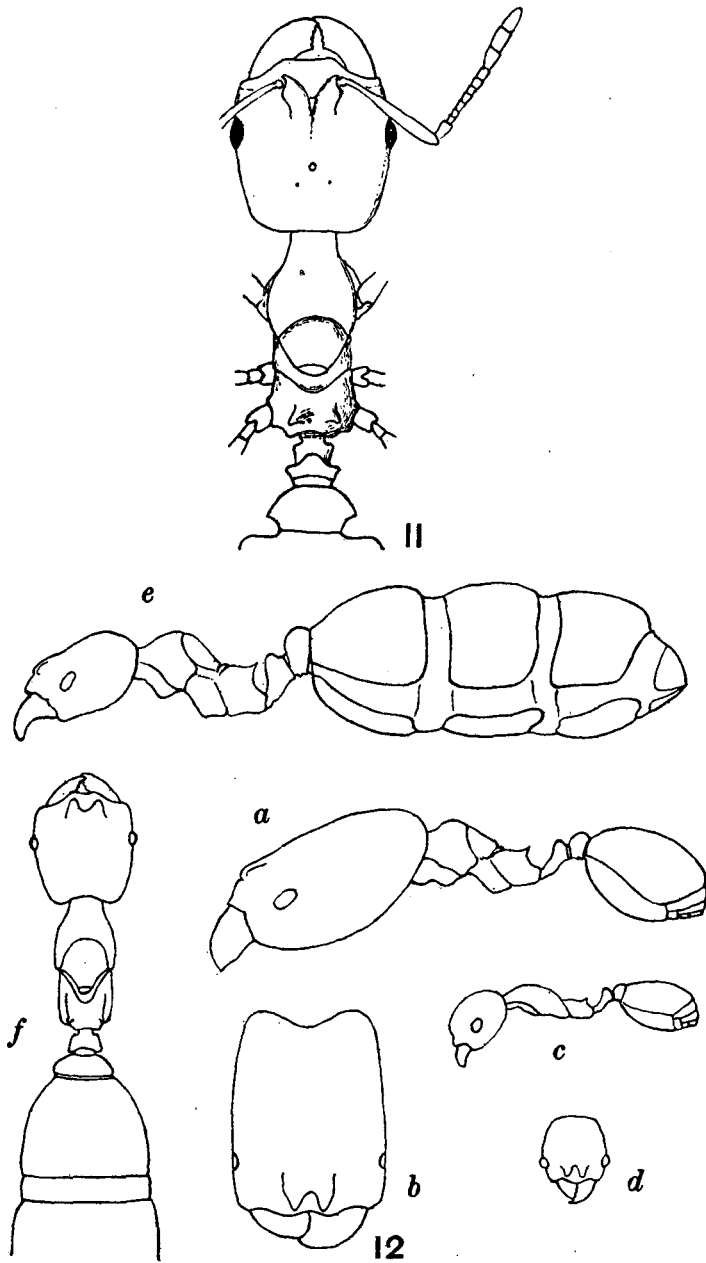
Figures 11 and 12

The three mermithergates kindly sent me by Vandel are very much alike and of nearly the same size (3 to 3.5 mm.), but they differ in certain significant particulars from the two types which he describes and figures. One of the specimens is shown in profile in figure 13, *g,* with the head in dorsal view
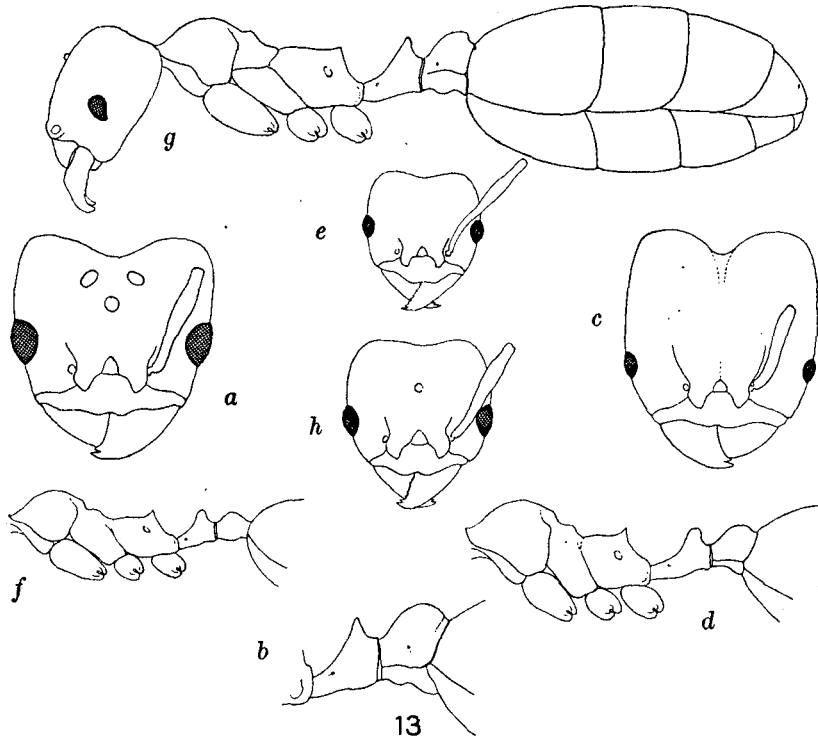
Fig. 13   *a,* head of queen of Pheidole pallidula Nylander; *b,* pedicel of same in profile; *c,* head of soldier; *d,* thorax and pedical of same; *e,* head of worker; *f,* thorax and pedicel of same; *g,* mermithergate (B); *h,* head of same.

in figure 13, *h.* The following description applies to all the specimens: The head is decidedly larger than that of the worker (*e*), but considerably smaller than that of the soldier (*c*), with larger eyes. There is an anterior ocellus, but no traces of posterior ocelli. The antennal scapes are stout as in the soldier and in proportional length to the head inter-
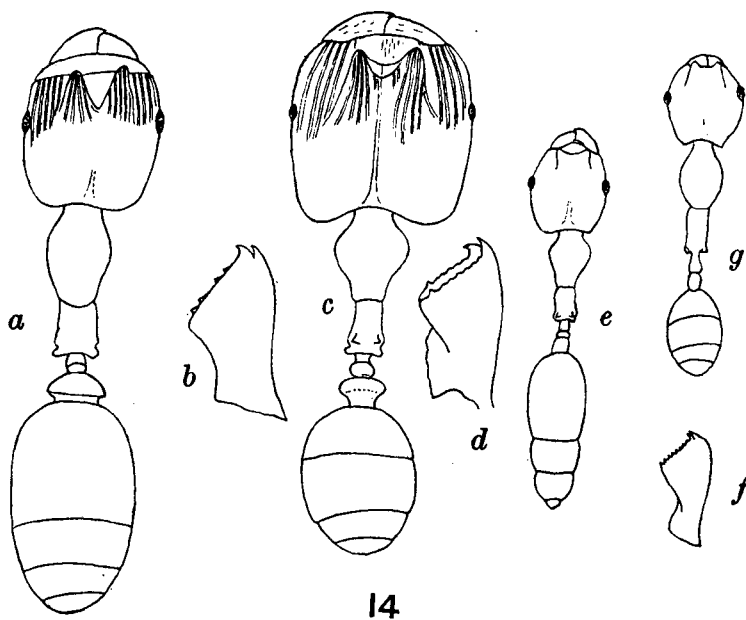
14
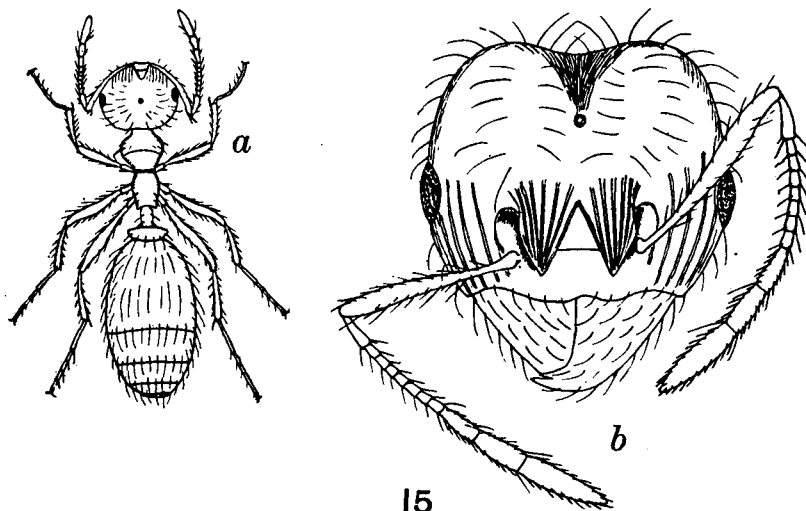
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Fig. 14   Pheidole pallidula Nylander.   a, mermithergate; b, mandible of same; c, normal soldier; d, mandible of same; e, mermithized worker; f, mandible of same; g, normal worker.   (After A. Vandel.)

Fig. 15   Pheidole pallidula Nylander.   a, mermithergate described as 'Ph. symbiotica'; b, head of same enlarged.   (After E. Wasmann.)

mediate between those of the worker and soldier. The mandibles, too, are intermediate between these two castes. The thorax is like that of the soldier (d), but somewhat longer, especially in the epinotal region, with less convex pronotal dorsum and humeri and less acute epinotal teeth. The petiole and postpetiole clearly resemble the corresponding segments of the queen (b), the petiolar node being more acute in profile and the postpetiole more convex, broader and with somewhat more angulate sides than in the soldier. The greater width of the postpetiole is also shown in Vandel's figure (fig. 14, a), but is not mentioned. The gaster, too, is of the elongate queen type and unlike that of all the other Pheidole mermithergates in showing no exposure of the intersegmental membranes or even of the basal portions of the sclerites. This smaller type of gaster is evidently due to the fact that there is only a single parasite in an ant and that the species infesting Ph. pallidula is smaller than those infesting Ph. commutata, absurda, atricolor, etc. The sculpture is intermediate between that of the soldier and worker; the cheeks have distinct longitudinal rugae, but these are shorter and feebler than in the soldier. The mandibles are subopaque and more striate, as in the worker and queen. The pilosity is longer, coarser, and more bristly than in the soldier and clearly more like that of the queen.

The following individual differences may be noted in the three specimens:

(A) has the head more rectangular than (B), which is shown in figure 13, h, and the ocellus is very small, though distinct. The posterior corners of the head are broadly infuscated. The antennae are, unfortunately, missing.

(B) The sides of the head, as shown in the figure, are distinctly convex, the median ocellus large and prominent. The color is pale like that of the normal soldier; the head smoother and more shining than in (A), the antennal scapes extending somewhat beyond the posterior corners of the head.

(C) is very much like (A) in color and like (B) in the shape of the head. The median ocellus is small; the antennal scapes do not reach the posterior corners of the head.

The study of these specimens shows that Vandel's mermithergate (fig. 14, *a*) is really much nearer the soldier type and, in the size of the head and mandibles, unlike any of the previously described examples of this anomaly. The specimens I received, however, are clearly like those which I described in Ph. commutata, except in the shape and dimensions of the gaster, and exhibit a similar mingling of worker, soldier, and queen characters and a similar preponderance of each of them in the three regions of the body. Vandel's specimen (fig. 14, *a*), as I have already remarked, falls within the normal range of variation of unparasitized soldiers of pallidula, so that one might doubt whether the modification is really due to Mermis, were it not that the narrower thorax (less convex pronotum and humeri) and the width of the postpetiole are similar to the modifications produced by Mermis in these structures in other species of Pheidole.

The three mermithergates above described also prove very definitely that Wasmann's 'Pheidole symbiotica' must be relegated to the synonymy as a pathological form of Ph. pallidula. One has only to compare figure 13, *g* and *h*, and figure 15, *a* and *b*, which is a copy of Wasmann's figure, to convince oneself of the identity of his "parasitic species in a very early stage of evolution" taken by Father Deckelmeyer in Portugal and the mermithized specimens taken by Vandel in southern France.

INTERPRETATION OF MERMITHIZED ANTS

The effects of mermithization in ants of different species and of different castes of the same species are sufficiently diverse to have led to differences of interpretation. Emery ('90), as we have seen, originally regarded the microcephalic mermithergates of Odontomachus haemotoda and chelifer as being perhaps distinct taxonomic varieties, though in the same paper he interpreted the mermithergates of Pheidole absurda as 'parthenogenetic females.' In my first paper ('01) I regarded the mermithergates of Ph. commutata as macroërgates, or giant workers, which owe their increased

stature to overfeeding during their larval stages. A few years later (1904), Emery, as a result of my observations, was able to show that the aberrant forms he described in 1890 were infested with Mermis and to advance his law of compensatory antagonism in the growth of the cephalic and abdominal regions of the ant-body. This he expressed as follows:

When the imago is developing in the full-grown ant-larva, the materials needed for the formation of the vitally essential organs, and among these notably the materials for the digestive and reproductive organs contained in the abdomen, are first called upon; the development of the external structure of the head and especially of the mandibles and muscles that move them is then regulated according to the amount of Anlage-material that has been left over. Phylogenetic factors may, perhaps, enter into the process, so that racially more ancient structures take precedence and atavistic structures are thus produced. It follows, therefore, that if during the metamorphosis of two larvae of the same size, the abdomen of one has a greater initial size than the other, the head of the former must diminish because a smaller quantity of the larval nutritive material remains for its development. In workers containing Mermis the parasite acts on the development of the head in precisely the same manner as an hypertrophied organ in the abdomen acts on the size of the body.

Wasmann's erroneous interpretation ('09) of the ocellate mermithergates of Pheidole pallidula as normal ergatomorphic females of an independent species of parasitic ant, Ph. symbiotica, needs no further comment.

Vandel's interpretation ('27) is essentially the same as Emery's, but the problem presents itself to him in a simplified form, because he recognizes only two kinds of mermithergates in Pheidole pallidula, namely, a morphologically unmodified worker and a form which is best described as a small-headed soldier with some admixture of worker and female characters in the thorax and pedicel. The three specimens which he sent me, however, are, as we have seen, intermediate between his two types and essentially like certain mermithergates of Ph. commutata, absurda, opaca, and atricolor. Owing to his having overlooked these forms and the admixture of worker

and queen traits in his soldier-like form his interpretation is necessarily restricted to the latter, which he believes to be actually determined during the pupal period of the ant. He summarizes his view as follows:

They (the observations) show that the differentiation of the Pheidole soldier is very late, since it is still amenable to modification during the course of metamorphosis. This delayed differentiation is certainly correlated with the recent phylogenetic origin of the soldier. The observations also show that the factor responsible for the differentiation of the soldier is one of nutrition. The denutrition provoked by the parasite has no effect on the general stature of the individual, which is definitively fixed at the end of the larval stage, but it modifies the proportions of the different parts of the body, so that at first sight the mermithergates are more like workers than soldiers, a resemblance which was precisely the reason for Wheeler's error. The head, which in ants with polymorphic workers, as we have seen, grows relatively much more rapidly than the body and which we may therefore regard as much more sensitive to the nutritive factor than the other body regions, is inversely the most affected by the alimentary deficiency occasioned by the parasite, and this deficiency accounts for the microcephaly of the mermithergate.

Although much of Emery's interpretation of 1904, supported as it was by many peculiarities in the normal polymorphism of the Formicidae, seemed to me convincing, I have come more recently to doubt its entire adequacy, and the scarcity of mermithized material and mixed character of most of the known specimens have prevented me from indulging in much discussion of the subject. In other words, the effects produced by Mermis on its hosts are really more heterogeneous and complicated than I had supposed, and it seemed advisable to postpone further interpretation till additional material had accumulated. The preceding descriptive pages show that we can distinguish at least six different types among the known mermithized specimens, namely:

Type I. Mermithogynes (Lasius).
Type II. Gynaecoid mermithergates (Ponerinae).
Type III. Soldier-like mermithergates (Pheidole pallidula).
Type IV. Ocellate ergatoid-gynaecoid mermithergates (Ph. commutata, atricolor, opaca, pallidula, and absurda).

Type V. Large non-ocellate ergatoid mermithergates (Ph.
          commutata, gouldi).
Type VI. Feebly modified workers (Ph. commutata, pallidula,
          atricolor, Camponotus cassius).

Of course, we shall have no adequate understanding of
these various types till ant larvae of various species and ages
can be artificially infected with young Mermis larvae and
reared to maturity under rigidly controlled experimental con-
ditions. Since many years will very probably elapse before
this can be accomplished, we are limited to inferences from
specimens found in the field or appearing in artificial nests.
In the meantime we may, I believe, clarify the problem some-
what by distinguishing and separately considering the va-
rious types and their probable dependence on differences in
the behavior of the parasite, the time of infection, etc.

  Before turning to an interpretation of the various types
of mermithized individuals, it will be advisable to consider
the parasites. It is certainly a remarkable fact that, though
species of Mermis and of several allied Nematode genera
infest many insects besides ants, no external appearances at
all comparable with those of the mermithogynes and mer-
mithergates are observed. Thus, Hagmeier ('12) was unable
to detect any morphological peculiarities in grasshoppers in-
fested with Mermis albicans.

  Strongly infected specimens of Stenobothrus species could be recog-
nized only because they dragged the abdomen, with its segments
drawn apart, and did not carry it erect like specimens free from
Mermis. The growth of both host and parasite was very rapid.

Glaser and Wilcox ('18), who observed in Vermont a very
high percentage (sometimes as much as 59 per cent) of para-
sitism of grasshoppers (Meranoplus) by Mermis ferruginea,
state that—

usually only one worm parasitizes a grasshopper, but by dissection
we have often found two or three and in one case we found forty.
Needless to say that when an insect contains so many worms the
abdomen is considerably swollen.

And Doctor Glaser writes me that—

the only detectable external appearance in grasshoppers parasitized by Mermis ferruginea was a tendency towards sluggishness. Wilcox and I could not see any size differences between the infected and uninfected individuals of Meranoplus femur-rubrum and M. atlanis.

May ('19) says of the Locustids Orchelimum and Xiphidium infested with Gordius robustus:

The parasite does not seem to impair very greatly the health of the host, for, unless the infection is very heavy, the infected specimens appear to be just as active as those that are not infected. In this respect the infection differs from an infection with Mermis. I have several times found specimens infected with Mermithidae to be sluggish.

Even in small Diptera Nematode infection produces no effects on external structures. Thus, concerning Sciara coprophila infested with Tetradonema plicans, Hungerford ('19) says:

Adults emerging from the jars containing infected maggots were in most cases parasitized. They could fly about, but were lacking in reproductive organs. The few uninfected flies contained normal reproductive organs, but there was little difference in the appearance, especially of the females, for the abdomens of parasitized flies were swollen with the mature nematodes.

Cobb, Steiner and Christie ('23) find that the larva of Agamermis decaudata enters the very young grasshoppers immediately after they hatch from the egg and that the growth of the parasite in the growing host is very rapid, "often increasing a millionfold in two or three months." These authors mention no external differences in infested specimens, but add:

Artificially infested grasshoppers containing six to eight Mermithids die in about eight days. In fact it may be doubtful if grasshoppers harboring more than one parasite ever reach maturity. The ovaries of infested females which do survive are vestigial, never producing functional eggs, and it is likely that the males are also rendered sterile. The exit of the nemas, sometimes at least, results in the death of the grasshopper, and there is every reason to believe that this is always the case.

To these cases of nema infestation we may add that of Asconema, which, according to Laloy ('06, p. 19), castrates its host, a small fly of the family Cecidomyidae. The fly, nevertheless, exhibits the normal behavior of oviposition, since she has been seen to insert her long ovipositor into the fissures of decayed bark and to extrude the Asconema embryos as if they were her own eggs. This is interesting in connection with a remark of Giard on sacculinized and otherwise parasitized Crustacea to the effect that the parasite, which may be said to usurp the place of the egg mass or ovaries, may bring about structural or behavioristic effects in the host analogous to those produced by the presence of the female reproductive elements. The distinctly female enlargement of the gastric sclerites and form of the petiole and postpetiole are very suggestive of a similar morphological tendency in many of the mermithergates.

While the foregoing accounts fail to present any evidence that nema infection produces an enlargement of the host, as I was led to believe ('01) from Montgomery's statement concerning Gordius, they show, nevertheless, that the host is neither dwarfed nor aborted and indicate that its development may even be accelerated.[3] But though castration and some denutrition of the host by the parasite are obvious, we are entirely in the dark in regard to other and more subtle physiological effects, such as those of the parasite's secretions on the growth and differentiation of specific tissues or organs. That there may be such effects, even in the direction of hypertrophy, is apparent from the studies of plant-infesting and gall-producing Nematodes, especially those of the genera Tylenchus and Heterodera. The hypertrophic influence of H. radicicola on the root cells of many plants are well known (Küster, '11; Caullery, '22). Küster cites Vuillemin and Legrain ('94) as finding that in the Sahara various garden vegetables (celery, beets, eggplants, and tomatoes) infected

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[3] Strickland ('11, '13) has, in fact, observed an increase in stature in Simulium larvae infested with Mermis. This case will be discussed in another connection (p. 216).

with H. radicicola grow more vigorously than non-infested plants. These authors surmise that the large, succulent root galls produced by the nemas act as storage reservoirs for water and thus stimulate the growth of the plants. Similar observations seem to have been made by Quéva ('96) on a Dioscorea. If these observations are correct, Vandel's statement in regard to the universally deteriorating effect of parasites needs qualification. In fact, the hypertrophic influence on the host of many gall-producing organisms and of certain gregarines and coccidians is so well known that my interpretation ('01) of the mermithergates of Pheidole of types IV and V as due to stimulation of metabolism and growth by the nemas is not altogether absurd, though I admit that it may be no longer necessary to account for the phenomena.

The peculiar and diverse forms of mermithized individuals among ants are probably attributable to the fact that both host and parasite present so many independent variables, and especially to the fact that the variability or instability of the host is much greater than that of other insects commonly infested with Mermis. This greater variability is due, of course, to the normal polymorphism of the female ant, which, so far as known, is the only sex that is mermithized. The parasite, too, is highly variable in its action, for we must bear in mind, first, that different species of Mermis are concerned in the phenomenon and that these may differ both in size and virulence. Thus the Mermis which infests Lasius queens certainly differs from those infesting the Neotropical Ponerinae, and those infesting the Neotropical Pheidoles probably belong to several distinct species and certainly differ from the species which parasitizes the Mediterranean Ph. pallidula. This species is decidedly smaller than the infested Neotropical species and its Mermis is also diminutive, so small, in fact, that it does not succeed in distending the gaster of its host to anything like the dimensions observed in any of the other species. Secondly, there must be considerable differences in the periods of infection. I have already

given reasons for rejecting Vandel's contention that the larval Mermis does not enter the larval, but only the prepupal ant, and we are justified in concluding, from what is known of the time of infestation in many other insects, that the Mermis larva may enter ant larvae of very different ages. There is, of course, nothing to prove that infection of very young female larvae or of male larvae may not be fatal, and it is not improbable that infestation of the large larvae that produce the fertile females, even in Pheidole, may produce no visible alteration of the external characters. This might account for the absence of adult mermithized males among ants and of mermithogynes among all the recorded species except those of the genus Lasius. Thirdly, the virulence of the parasite may be expected to vary directly as its numbers. Certainly, some mermithergates contain several of the parasites, while in others, e.g., those of Ph. pallidula, the effects, according to Vandel, are constantly due to the presence of a single Mermis. Since, however, all of these variables are exhibited in the Mermis infestations of other insects without producing external morphological alterations of the host, we must conceive the peculiarities of mermithized ants to be mainly conditioned by the unusual instability of the ant larva. According to the most probable theory of polymorphism in the social Aculeata, the young female larva arises from a fertilized ovum and is at first in a neutral, or undifferentiated condition. Later, differences in feeding determine whether the adult larva will produce a worker, a soldier, or a fertile female or queen, imago. In different forms with only two female castes the 'switchover' in determination to the worker phase may occur at different times; in such ants as Lasius and Crematogaster, in which the worker and queen are of very different size and structure, it must intervene much earlier than in the Ponerinae, which have very similar worker and fertile female castes. In Pheidole the young larva is probably very early deflected toward the worker phase, and if this does not occur, the larva proceeds in its development as a soldier-queen larva. This may later differentiate by

another switchover into a soldier or continue its development as a queen larva. These considerations are confirmed by Emery's observations ('18, '21) on the development of Aphaenogaster testaceopilosa spinosa and Pheidole pallidula. In the former, which has no soldier caste, the worker larvae are fed with fragments of insects by the worker nurses, but the fertile female larvae are given regurgitated food (or saliva?). Concerning Ph. pallidula, he says ('21):

In 1916 I repeated much the same experiment on a colony of Pheidole pallidula, the only species of European Myrmicine which has the soldier caste sharply separated, without transition, from the worker caste. Having removed the mother queens from the colony July 8, I noticed 20 days later that three of the larvae, larger than the others and distended like bladders, were literally covered with workers, so that the mass of ants had to be disturbed in order to see the larvae. The three vesiculate larvae metamorphosed into soldiers during the first ten days of August. In Pheidole, therefore, the method of rearing the soldiers differs profoundly from that of rearing the workers. What are the workers doing while they are covering the soldier larvae? I do not know. I have seen them behaving in the same manner towards the male larvae which are also vesiculate, and I surmise, though I cannot substantiate the statement, that the female larvae are treated in the same manner. Since there is no feeding of fragments of insects to the vesiculate larvae I infer that they are fed by regurgitation.

My own observations on colonies of Ph. instabilis in artificial nests confirm Emery's conclusions. The larvae of the soldiers, males, and queens may be readily distinguished from those of the workers not only by their greater size and more globose or broadly ellipsoidal shape, but also by their translucency—a peculiarity due to the great distention of their stomachs with liquid food.

The putative courses of development in ants with dimorphic and trimorphic female castes are indicated in figures 16 and 17. Not improbably, the incidence of Mermis infection at different periods during the life of the larva may account for arrests in development or alterations in structure like those exhibited by the six different types of mermithergates

above distinguished. To a consideration of these we may now turn.

Type I. In the case of the mermithogynes of Lasius we are justified in assuming that the young Mermis larva enters the mature or nearly mature female ant larva, and not the pre-
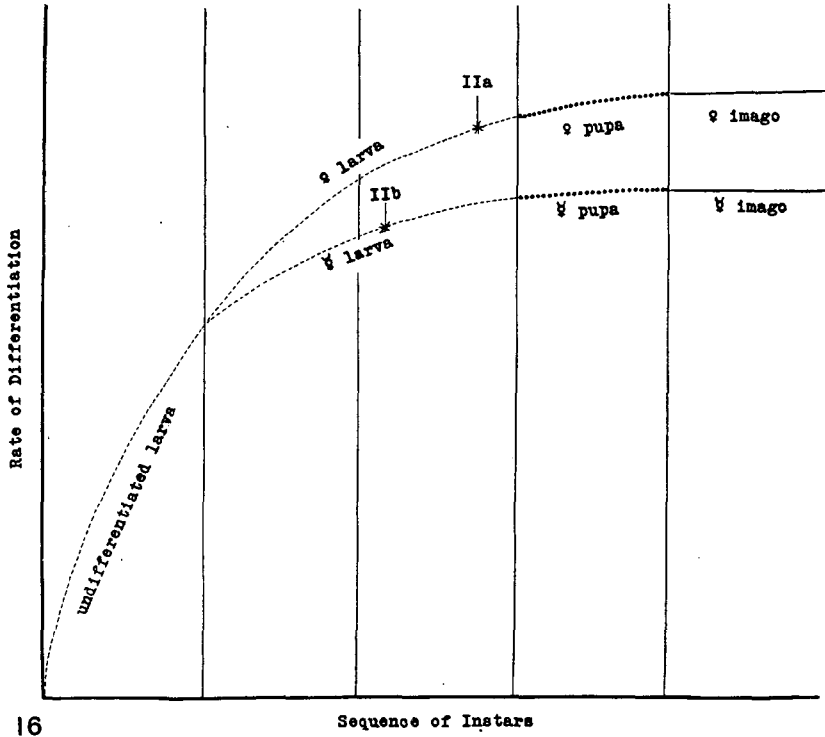
Fig. 16 Schematic developmental curve of a ponerine ant, with dimorphic female (worker (☿) and queen (♀)); II a and II b, putative points of infection of second-type mermithergates by Mermis larvae.

pupa, since the cocoon is spun by the larva and it is very improbable that the Mermis waits till this obstructing envelope is completed before perforating the very delicate integument of the host. Moreover, the peculiarities of the mermithogynes are so slight that they could all result from late infection of the larva and from the activities of the parasite (withdrawal

of nutriment or production of inhibiting secretions) during
the prepupal, pupal, and early imaginal stages.   It is true
that nude queen pupae of Lasius have been observed, but their
occurrence is too rare to account for the rather frequent de-
velopment in England and North America of mermithogynes
by infection in the prepupal stage.   The incipient growth of
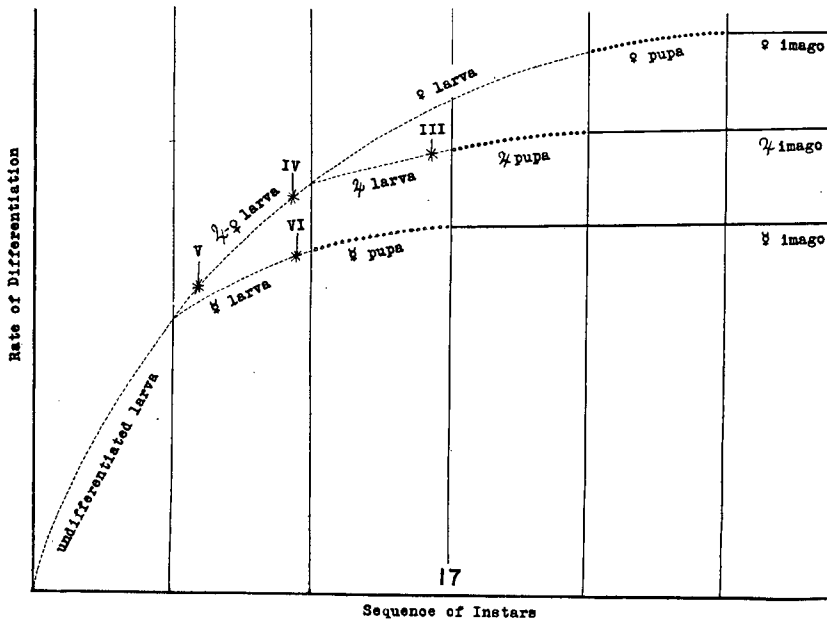
Fig. 17   Schematic developmental curve of Pheidole, with trimorphic female
(worker ($\female$), soldier ($\jupiter$) and queen ($\venus$)); III–VI, putative points of infection
of third to sixth types of mermithergates by Mermis larvae.

the Mermis during the pupal stage may explain the diminu-
tion of the head and thorax, and Emery's law of compensa-
tory growth in the host might be adduced in this connection.
The development of the wings may be intimately correlated
with that of their musculature, so that trophic disturbance
and underdevelopment of the latter may account for the ab-
breviation (brachyptery) of the former.   The observations of
Cuénot and Mercier ('24) on Diptera and of Poisson ('24) on

aquatic Hemiptera, however, somewhat diminish the proba-
bility of this correlation, since they failed to find it in the
brachypterous species which they studied. The degeneration
of the vibratory muscles of the wings of female ants immedi-
ately after deälation, as observed by Janet ('07) and C. Pérez
('12), is really a different phenomenon, though it proves that
there is a very intimate functional connection between the
presence of the fully developed wings and the retention of
their musculature.

The interpretation of the Lasius mermithogynes has been
approached by Strickland ('11, '13) from a different angle.
He made a careful study in my laboratory of the infestation
of Simulium hirtipes and bracteatum larvae by Mermis and
found that—

the worm lives either singly, or in considerable numbers, coiled up
within the body cavity of its host, where it occupies the ventral por-
tion of the somewhat swollen abdominal region. When one worm is
present it measures about three centimetres, which is nearly three
times the length of its host. The greatest number of worms found
in a single larva was twelve. In this case none attained to a greater
length than 1 cm. (The most striking effect of these parasites upon
their larval host is that they so far inhibit the development of the
histoblasts that pupation becomes impossible. This suppression of
pupal and adult organs is accompanied by a slight increase in the
size of the larval tissues, for parasitized larvae were from 2 to 3
mm. longer than their healthy companions.) This condition is op-
posite to Prothetely, which name Kolbe ('03) ascribed to the several
recorded cases in which larvae of various orders had their histoblasts
so accelerated that the pupal, or in some cases adult organs appeared
as external structures in the as yet immature larvae.

Strickland therefore called the phenomenon in Simulium
'metathetely' and accounted for it in the following manner:

A study of the cases of prothetely now on record shows that they
were all produced under artificial conditions. This would suggest
that it is due to some pathological disturbance, which has caused
an excessive stimulation of the enzymes, whose action brings about
the multiplication of adult tissue forming cells, without appreciably
affecting those of the larval tissues. It then follows that (there are
two sets of enzymes concerned in the maturation of holometabolic

insects, one of which may be termed the 'larval enzymes' and the other 'adult enzymes.' The suppressed growth of the histoblasts in parasitized Simuliidae would then be due to the worm decreasing the stimulating action of the adult enzymes by impoverishing them either in quality or quantity.

In this connection Strickland called attention to the brachyptery of Lasius mermithogynes as a phenomenon of the same kind, though the effect of the Mermis is feebler. The nema does not prevent the imaginal development of the fly, but its inhibitory action on the imaginal discs of the wings and their musculature is shown in the uniform brachyptery and stenothoracy of the infested individuals. Von Lengerken, in a recent paper ('24), has also interpreted these conditions in Lasius mermithogynes as due to metathetely.

Up to the present time, no mermithogynes have been seen among myrmicine ants. In 1917, I described from two localities in south and northwest Australia a species of Monomorium, M. (Notomyrmex) subapterum and its var. bogischi, in which both pairs of wings are so greatly reduced in the females that they bear an astonishing resemblance to the Lasius mermithogynes. When I first examined the specimens I was sure that they were the normal females of the species and that their brachyptery could not be due to infestation by Mermis or other parasites. Nevertheless, a few of them were dissected without revealing any traces of nemas, but I failed to mention this fact in my paper. In order to remove all doubt in regard to the matter, I have again carefully dissected three of the brachypterous females. Their viscera are perfectly normal, though the ovaries are small, owing to the unfecundated condition of the specimens. In all of them the fat-body is voluminous and well-developed and in none of them am I able to detect any traces of Mermis or other parasites. The brachyptery of M. subapterum must be due, therefore, to some normal inhibiting factor which intervenes to prevent the full expansion of the wings when the insect emerges from the pupa. In other words, we are concerned merely with a case of normal brachyptery, or subaptery, like those observed in so many insects of all orders.

Another case that comes to mind in connection with the mermithogynes is that of the bumblebee infested with the singular Nematode Sphaerularia. Here the conditions are really very different, however, for though the host is a social insect and only the female is attacked as in Lasius, the nema is believed to bore its way into the adult bee while she is taking up her abode in the ground before overwintering. Hence there is no modification of the external structure of the host nor of her organs of flight, but only a destruction of her ovaries (parasitic castration). It may be conjectured that, if the Sphaerularia entered the unstable or polymorphic larva instead of the adult bee, the latter might exhibit peculiarities comparable with those of Lasius mermithogynes.

Type II. What I have called the gynaecoid mermithogynes of the Ponerinae are characterized by their small, posteriorly narrowed heads and certain distinctly female traits, notably the more voluminous gaster, and in certain species (Odontomachus) the minute ocelli and the shape of the petiole (Neoponera, Pachycondyla). In the normal development of the Ponerinae we must, I believe, assume that the differentiation of the neutral larva into either a worker or a female larva occurs comparatively late (fig. 16). We may suppose, moreover, that the more gynaecoid, ocellate mermithergates arise from rather advanced female larvae infected at some point near (II a), whereas the less gynaecoid, non-ocellate forms arise from somewhat less advanced worker larvae infected at a point near (II b). If this interpretation is accepted, however, it will be necessary to assume that certain larval characters (thoracic structure, ocelli) may be inhibited by the action of the parasite, though the general development is accelerated and pupation becomes precocious. This supposition would also have to be made in the interpretation of the following types of mermithergates.

Type III. This type, which is represented only by the mermithized specimen of Pheidole pallidula described and figured by Vandel (fig. 14, *a*), has been sufficiently discussed. It arose, in my opinion, from a soldier larva infected by

Mermis at a point near (III) in figure 17 and therefore just before pupation.

Type IV. This is the most interesting type, because of the distinct mixture of worker, soldier, and queen characters which it exhibits. It may be conceived to arise from a soldier-female larva at some point near (IV) in figure 17, before the larva has been deflected toward either the soldier or queen courses of development.

Type V. The appearance of this type, which is that of a giant worker, is best shown in the mermithergate of Pheidole gouldi (fig. 7, a, b). I believe that it may have arisen from the infection of a young soldier-female larva which had not advanced far beyond the point (V) in figure 17, at which feeding by regurgitation had been begun.

Type VI. The feebly modified mermithergates of this type are, of course, most easily interpreted as arising from differentiated worker larvae (VI, fig. 17). In many of the specimens, however, there are adumbrations of queen or soldier characters, especially in the slight enlargement of the petiole, postpetiole, and gastric sclerites, so that if these mermithergates arise at a later larval stage than I have indicated in the diagram, we must suppose that the parasite actually revives lingering morphogenetic tendencies that have become obsolete in the normal, uninfected, adult worker larva.

This latter supposition brings us to a consideration of the possibility, briefly suggested by Emery ('04), that phylogenetic or atavistic factors may be involved in the production of the mermithergates. We may, indeed, inquire whether the third to sixth types of these anomalies represent phylogenetic stages or conditions in the more ancient Myrmicine ants from which the genus Pheidole is supposed to be descended. Now there are several genera which are very closely related to Pheidole and represent more primitive conditions of the worker caste in that it is either monomorphic, though somewhat variable in stature (Aphaenogaster, Novomessor, Stenamma, Goniomma, Oxyopomyrmex) or polymorphic, with a series of intergrading forms, but with the head of the

major or maxima workers decidedly smaller than in Pheidole (Messor, Veromessor). Apart from the presence of ocelli or ocellar pits, the mermithergates of types IV to VI bear much the same relation to the normal workers that the major workers of certain species of Aphaenogaster and Messor bear to the cospecific minor workers. And since there are some species of Myrmicinae (Pheidologeton, Atta) in which the anterior ocellus is clearly present in the worker maxima or soldier and others in which small ocelli are present even in the ordinary workers (Pseudomyrma, Tetraponera, Pachysima), it is not improbable that the ancestral genus from which Pheidole was derived may have possessed moderately poly-morphic workers, with traces of ocelli in the largest indi-viduals. These may properly be called 'macroërgates,' and this was precisely the term which I applied to the mermither-gates of types IV and V in my paper of 1901. Apart from the distention of the gaster by the Mermis, their resemblance to Aphaenogaster workers is indeed very striking.

But whether we regard the more extreme mermithergates as representing a new and unprecedented worker caste pro-duced by parasitic infection or as representing the revival of an ancient caste which became converted during phylogeny into the present huge-headed Pheidole soldier, we are justified in stating that Emery's law of compensatory antagonism be-tween the growth of the head and the gaster does not afford a complete explanation of the peculiar mixture of certain features of all three castes in varying proportions in the mermithized specimens of types II to VI. The correctness of my interpretation of these forms as due to differences in the developmental stages of the larvae at the time of infection can be determined only by experiment and the examination of much more material than has been available heretofore. The problem is, of course, greatly complicated by the fact that the worker nurses may themselves be said to subject the infected, as well as the plastic non-infected larvae, to experiments in nutrition and denutrition and by our lack of a knowledge of the precise nature of these experiments.

DISCUSSION

Apart from their bearing on the problem of the physiological effects of parasites on their hosts, the mermithergates described in the preceding pages are of considerable interest for two reasons: first, because of their importance in connection with the general problem of caste development, or polymorphism in the social Hymenoptera and other insects, and, secondly, because they are very suggestive in connection with certain aspects of intersexuality. The fact that the mermithergates of such ants as Pheidole often exhibit an anomalous mixture of traits characterizing all three of the female castes affords valuable confirmation of the theory that the fertilized eggs all have essentially the same genetic constitution and that the resulting larvae develop into workers, soldiers, and fertile females or queens, because they are subjected to three different trophic conditions by their worker nurses. The Mermis, especially if it enters a partially differentiated larva, must be supposed to disturb its metabolism and histogenesis in such a manner as to revive recessive traits which, under normal trophic conditions, would fail to make their appearance in a particular caste and to suppress or inhibit others which, under these conditions, would manifest themselves.

From another point of view the mermithized individuals may be regarded as forms intermediate between the normal, sharply differentiated castes of the species to which they belong. Thus, the series of mermithergates in Pheidole may be said to represent intergrades, or intercastes, between the normal worker and soldier, though they are for the most part unlike the intergrades which occur normally in colonies of Ph. instabilis, rhea, vasliti, etc. And even the mermithogynes of Lasius may be said to show a feeble approach to the worker caste in the abbreviation of the wings and narrowing of the head and thorax. We may, therefore, distinguish two kinds of intercastes in ants: those which occur normally as the result of differential feeding and those due to parasitic infection, and hence pathological. To the former belong the

intermediates between the minor and major workers, or between the workers proper and soldiers in a number of genera of Dorylinae, Myrmicinae, Dolichoderinae, and Formicinae. These annectent forms combine in varying proportions the characters of the extreme castes between which they lie (Atta, Pheidologeton, Dorylus, etc.). We also have intercastes, represented by the ergatoid, or ergatomorphic females, which connect the largest workers with the queens in a number of genera (Ponera, Myrmecia, Phyracaces, Leptothorax, Monomorium, etc.).

It is interesting to note the occurrence among ants of pathological castes of parasitic origin besides those produced by Mermis. Many years ago (1907), I described the effects of the Chalcid Orasema viridis on larvae of Pheidole instabilis. In this instance the infected worker and female larvae may become peculiar abnormally microcephalic pupae (phthisergates and phthisogynes), but are unable to attain the imaginal stage. More striking examples of intercastes are the pseudogynes of Formica sanguinea and F. schaufussi, which develop in colonies infested by the singular symphilic beetles of the genera Lomechusa and Xenodusa and exhibit distinct intergrades between the normal worker and queen even to the extent of occasionally possessing vestigial wings. I have recorded the occurrence of pseudogynes in other species of Formica (rufa and fusca) and in Myrmica schencki ('07), and Emery has found them in Camponotus senex ('00), Pheidologeton diversus ('04) and Technomyrmex albipes ('24). Though all these cases would seem to be pathological, they can hardly be due to a definite parasitic infection of the colonies as in F. sanguinea and schaufussi.

Other social Hymenoptera may also have intercastes, e.g., the bumblebees. Their adult colonies often present a more or less perfectly graded series of individuals between the smallest workers and the queen. In the honey-bee intercastes between the workers and queen have been obtained experimentally by transferring worker larvae two and one-half to four and one-half days old to queen cells. Von Buttel-

Reepen ('11) describes and figures several of these individuals which he and Klein ('04) succeeded in rearing, and calls attention to the fact, familiar to bee-keepers since the time of Dönhoff ('84), that after the queen has been removed from the hive, the workers set about enlarging some of the worker cells, and endeavor to convert the contained larvae into queens. "According to the age of the larvae more or less well-developed queens emerge; the older the larvae (when transferred from worker to queen cells), the smaller and more worker-like the queens." Here the intercastes have a pathological origin, since they are produced in nature only after the hive has been castrated, i.e., has lost its reproductive organ, the queen. It is conceivable that pseudogynes may sometimes arise among ants under similar conditions, though more frequently one or several adult workers are abundantly fed and thus converted into imperfect egg-laying substitutes for the missing mother of the colony.

Among the termites, also, intercastes are well known as normal intermediates connecting the reproductive and worker castes, e.g., the 'second-' and 'third-form' reproductive adults and between the reproductive and soldier castes, e.g., the egg-laying soldiers of Archotermopsis described by Imms ('19) and those of Termopsis described by Heath ('27). In certain species of Termes, moreover, there may be soldiers of different sizes in the same colony. These various forms are clearly comparable with the intercastes of ants, since they are adult individuals and not nymphal stages, which in termites are, of course, transitional in a purely ontogenetic sense.

It has been shown recently that anomalous castes analogous to the mermithergates may be produced by certain parasites in termites and that the forms thus produced were at first mistaken not only for distinct species, as in the case of Wasmann's 'Pheidole symbiotica,' but as representing a distinct genus. The termite parasite, however, is not a Nematode, but the larva of a Muscid fly belonging to a genus and species still unknown. It was found by Kemner ('25 a, '25 b) occupying nearly the whole of the cranial cavity in a few

soldiers of two species of East Indian termites which had been described by Holmgren as Gnathotermes aurivillei and havilandi. Kemner was able to show that the types of these species are merely soldiers of Termes malaccensis modified by this peculiar kind of parasitism, so similar to that of the Phorid fly Apocephalus pergandei in the heads of our North American carpenter ants (Camponotus pennsylvanicus). In the infested termites, the head is smaller and more rounded, the mandibles and clypeus shorter and more pointed than in the normal soldier of malaccensis, while the number of antennal joints is increased from seventeen to nineteen. The body is also affected, since the thoracic nota are distinctly broadened and the abdomen is more hairy. More recently ('26), Silvestri has also described similar head deformations by similar parasites in Termes gilvus soldiers from the Philippines. That the Muscids responsible for these effects must be widely distributed in the Old-World tropics is shown by the following remark in a letter just received from Dr. Alfred A. Emerson:

Sjöstedt (1926, Pl. 3, Figs. A1 to 5a and text fig. 21) drew and described five different soldiers of Acanthotermes acanthothorax, which to my mind represented the acme of soldier polymorphism, the soldiers apparently belonging to two distinct types, each with a size series. One of these, however, I found to be due to a large parasitic fly larva in the head, which caused structural modifications somewhat similar to those recently described by Kemner and Silvestri in Macrotermes soldiers from the Orient. Another was a simple size variation, so the insect actually has only three forms of soldiers of two general types. If I had not discovered the parasite, I surely would have been talking soon of this remarkable case of polymorphism and I had even been pondering on theories for its explanation. Incidentally, it is a new type of parasite for Africa and of interest apart from polymorphism.

The term 'intercastes' may obviously be applied to the many well-known intermediate forms which connect the extreme, or 'high' and 'low' males of a number of Coleoptera belonging to the families Lucanidae, Scarabaeidae, Cerambycidae, Elateridae, Curculionidae, etc., certain wasps (Synagris

cornuta), Forficulidae, fig insects of the genus Philotrypesis, etc., which exhibit peculiar polymorphic, or heterogonous development of the mandibles, cephalic and prothoracic horns, antennae, legs, or cerci. To the same group of phenomena belong the antlers of deer and the horns of Titanotheres among mammals. Many of these cases have been recently reviewed by Champy ('24). Julian Huxley ('27) has properly included among them the polymorphic workers of ants (Camponotus gigas and Anomma nigricans) which also conform, as he maintains, to his equation for simple heterogony, namely, $y = bx^k$, where $y =$ the organ, $x =$ the rest of body, and b and k are constants. He concludes that the—

simplest explanation for polymorphic neuters in ants is that they are determined by varying time of pupation, the 'micrergates' being individuals which are caused by the nurses to pupate when small, the largest soldiers being individuals, of the same genetic constitution, which are allowed to grow to maximal size as larvae. Discontinuity between soldier and worker types would then be caused by discontinuity of treatment of larvae, not by differences in genetic constitution. (It is probable that this does not apply to termites, in which the different castes differ qualitatively, and not only in absolute size and relative proportions.)

This parenthetical remark seems doubtful in the light of Emerson's recent studies on Constrictotermes ('26) and those of Heath on Termopsis ('27).

Other phenomena that unmistakably resemble the normal intercastes and especially those due to mermithization are the gynandromorphs and intersexes which are receiving so much attention in recent literature. These intergrades clearly bear much the same relation to the two normal sexes as the intercastes to the typical castes which they connect, since we are concerned in both cases with fusions or mosaics of characters normally developed only in the extreme differentiated forms. Goldschmidt, on the basis of his observations on gypsy moths, distinguished intersexuality sharply from gynandromorphism. He says ('27):

Intersexuality consists, of course, in the fact that at a particular moment in the development, the turning point (Drehpunkt), the sex of the organism is reversed, and that the development, which up to that time had begun with one sex, henceforth terminates with the other.

He therefore conceives intersexuality to consist in the ontogenetic and physiological acquisition by one sex of characters belonging to the other. Gynandromorphism, however, he regards as a mosaic or chimera-like anomaly due to irregularities in the distribution of the genes during the earliest cleavage stages, or to what Crew ('26–'27) calls "disharmony in the distribution of the sexual genotype." But it is very doubtful, as Cockayne ('15), de la Vaux ('21), Crew ('26), and Prochnow ('27) suggest, whether this distinction can be rigidly maintained. I therefore agree with some of these authors in adopting a broader definition of the term intersexuality and in including under it all the phenomena in which an individual organism (Metazoon or Metaphyte) reveals more or less bisexuality either in its primary (gonadic), secondary (somatic), or tertiary (behavioristic) sexual characters. These phenomena, which are extraordinarily numerous and diverse, may be grouped as follows:

1. All cases of normal hermaphroditism and normal sex reversal (protandry, protogeny).

2. The cases of gynandromorphism.

3. The cases of serial intersexuality, or intersexuality sensu stricto (in Goldschmidt's sense).

4. The cases of intersexuality due to parasitism (stylopization of bees and wasps; aphelopization of Membracids; sacculinization of crustacea, etc.).

5. The cases of normal (taxonomic) intersexuality in ants and bees (Megachile).

The cases included under 2, 3, and 4 are due to unusual disturbance of development either in its earlier or later stages and are therefore clearly pathological. They may be produced by such different conditions as hybridization, inbreeding, parasitic castration, peculiar food or temperatures, or mechanical shock.

It has usually been supposed that gynandromorphs must be due to nuclear or chromosomal disturbances during fecundation, and Morgan ('05), Boveri ('15), Morgan and Bridges ('19), and Goldschmidt ('23) have elaborated well-known hypotheses to account for the phenomenon on this basis. Von Dönhoff, as early as 1860, and myself ('03) were inclined to derive gynandromorphs from pairs of fused oocytes, i.e., eggs before fertilization. Doncaster ('14) found in moths binucleate oocytes which might naturally be conceived to have arisen from fusions of oocytes. According to Goldschmidt ('23), Goldschmidt and Fischer ('27), and Goldschmidt and Katsuki ('27), Doncaster's hypothesis furnishes the only satisfactory explanation of the peculiar hereditary and usually bilateral or dorsoventral gynandromorphism occurring in both the larval and adult phases of certain races of silkworms. The Whitings ('27) have endeavored to explain gynandromorphs in Habrobracon as due to fusions of ootids. All these various hypotheses have been seriously invalidated by facts that have come to light within recent years. First, we now know that gynandromorphs may arise from parthenogenetic eggs, as has been shown by Pantel and de Sinéty ('08) and Nachtsheim ('23) in the Phasmid Carausius and by Banta ('16, '18) and de la Vaux ('26) in Cladocera. To these cases, of course, any hypothesis depending on an abnormal distribution of spermatic elements can have no application. Secondly, the hypotheses of fused oocytes or fused ootids would seem to be inapplicable to cases like the honey-bee, in which Rösch ('26) has obtained gynandromorphs like those of the famous Eugster hive by simply undercooling fertilized eggs. Furthermore, that gynandromorphs may arise as late as the larval stages has been shown by Kosminsky ('11, '24 a, '24 b, '27), Goldschmidt ('22), Emeljanoff ('24) and Golowinskaya ('27), who obtained such anomalies by subjecting gypsy-moth caterpillars to unusually high or low temperatures. Kominsky also claims to have obtained similar results by means of feeding. Still more surprising is Poulton's report ('27) on the experiments of

von Sommern, who produced several gynandromorphs of the butterfly Papilio dardanus by simple mechanical shock "at the time during which the larval skin is being cast and the pupa still soft and unset." It would seem, therefore, that we have greatly underestimated the number and nature of the conditions which may bring about a scission, or dissociation of the male and female genetic Anlagen common to all cells of the soma, and thus produce gynandromorphs and intersexes.

The intersexual forms due to parasitic infection are most interesting in connection with the mermithized ants described in this paper, because in both sets of phenomena we have parasitic castration and a disturbance or mingling of the normal secondary and tertiary sexual characters. Caullery ('22) was, I believe, one of the first to point out that the sacculinized crabs, which have long been known from the researches of Delage, Geoffry Smith, Potts, and others, are really intersexes in Goldschmidt's sense. Salt ('27), in a very valuable paper, has recently reviewed all the important literature on this subject and has demonstrated that in specimens of a number of bees (Andrena) and wasps (Odynerus, Ancistrocerus, Sphex) the effects of stylopization, and in Membracids the effects of infestation by Aphelopus (Kornhauser, '19), etc., may be interpreted in the same manner. Salt says:

In the first place, we are correct in applying Goldschmidt's hypothesis to stylopized individuals, for they may be considered, under his definition, as intersexes. That they developed normally as individuals of one sex up to the time of their infestation may be taken for granted, and in that they show finally, not a mosaic, but a mingling of male and female characters, a change must have occurred in the intervening time which prevented the normal development of certain characters and yet permitted the expression of characters belonging to the other sex. This change which is effected by the strepsipteron, is the counterpart of the 'switch-over reaction' of Goldschmidt.

Attention may also be called to the fact that in some ants and bees certain intersexual conditions involving secondary sexual characters become normal peculiarities of the species.

Among ants, as in most Aculeates, the normal number of antennal joints is twelve in the female, both fertile (queen) and sterile (worker), and thirteen in the male, but in certain genera the male may have the same number as the female. This is the case both in such non-parasitic genera as Metapone, Tetraponera, Pachysima, Pseudomyrma, Stereomyrmex, and Cataulacus and in the peculiar workerless parasites Anergatides (female 12, male 12), Epoecus (female 11–12, male 11–12), Anergates (female 11, male 11), and Pseudoatta (female 11, male 11). In all these genera, moreover, there is a pronounced tendency for the male to resemble the female in other somatic characters as well. In other words, the males of these ants are decidedly gynaecomorphic. Occasionally, moreover, colonies of species in which the males have thirteen-jointed antennae, may contain numerous specimens in which the number of joints is reduced to twelve. Emery ('24) has called attention to six of these intersexual males in a series of Pogonomyrmex molefaciens var. marfensis Wheeler in his collection. I believe that I must have sent him these specimens many years ago, because on reexamining a series of marfensis which I took from a colony June 8, 1902, at Fort Davis, Texas, I find that I have also retained six males with twelve-jointed together with eight having thirteen-jointed antennae. Emery's specimens very probably belonged to this same colony which must have had a very pronounced tendency to produce intersexual males.

The males of ants may also take on the characters of the sterile females, or workers, and thus become ergatomorphic. Thus, in the genus Ponera, most species of which have highly specialized males, we find certain species in which the males are normally apterous and distinctly worker-like in all the characters, except the reproductive organs. In the Mediterranean Ponera eduardi Forel there are two male forms, one of the normal winged type and the other wingless and distinctly ergatomorphic, though possessing thirteen-jointed antennae. In some other species, however, e.g., P. punctatissima Roger, ergatandria Forel and mina Wheeler, the male

is always very much like the worker in somatic structure
and even has twelve-jointed antennae. Similar conditions are
also found in certain species of Cardiocondyla, e.g., in C.
batesi Forel var. nigra Forel, which has two forms of males,
one winged and rare, the other ergatomorphic and common,
and C. stambuloffi and C. nuda Mayr var. mauritanica Forel,
in which the only known male resembles the worker. Santschi
('07) was able to make an interesting observation on mauri-
tanica, which shows that even the tertiary, or behavioristic
characters of the ergatomorphic male may approach those
of the sterile female. He says:

I installed this formicary, composed of some twenty workers with
larvae and pupae, a few females and a single ergatomorphic male
found in the nest. Since the ants persisted in hiding their brood
under a small pile of sand, I frequently disturbed them in order to
see what they were doing and was able to observe repeatedly that the
male also seized the larvae and carried them to a place of safety in
the same manner as the workers. I am not aware that any male
ant has been seen to labor like a common worker, and if the fact is
confirmed for other ergatomorphic males, it would be of special
importance as definitively proving that this singular male is merely
a worker always capable of fecundating, just as the ordinary worker
is able to lay parthenogenetic eggs.

This observation is of interest in connection with the pe-
culiar ambivalent behavior which the Whitings ('27) have
observed in gynandromorphs of Habrobracon.

In the ants cited in the two preceding paragraphs the male
has acquired female characters, but there are certain species
of the tribe Tetramorii in which the female appears to take
on male characters. Usually, the females and workers of the
Tetramorii have twelve-jointed antennae, but in occasional
species the number may be eleven or even ten. The males have
ten-jointed antennae—a condition which has arisen from the
fusion of four joints to form the second funicular joint.
This is indicated by the considerable length of the joint and
the fact that in one African species, Tetramorium solidum,
the antennae have twelve joints, and in another, T. emeryi,
thirteen joints, i.e., the primitive number. The genus Dec-

amorium, however, has ten-jointed antennae in both sexes. It would seem, therefore, that the females of the latter genus and those of the genus Tetramorium, which have ten-jointed antennae, are to be regarded, at least so far as this character is concerned, as normal intersexes.

My attention has been recently called to several leaf-cutting bees (Megachilidae) which have female intersexes comparable with those of ants. In 1911, Cockerell erected the genus Androgynella for an Australian bee, previously described by him as Megachile detersa, because the female possessed thirteen-jointed antennae and had the anterior coxae spined like the male, but, unlike the females of Megachile, lacked the ventral scopa of the abdomen. He appended the following remarks to his description:

Mr. R. Turner examined 14 female specimens in his collection and all had 13-jointed antennae and wholly lacked a ventral scopa. It is therefore certain that this is a normal condition and must represent an early stage in the evolution of a parasitic series, like those of Coelioxys and Stelis. From the standpoint of genetics, it is an extraordinary case, since the female seems to have dropped her secondary sexual characters and thereby assumed those of the male, which were present in her gametic constitution. It is noteworthy that the sting, a modified primary character, is retained. It appears that in Megachile the female is heterozygous for the secondary sexual characters, with the female characters dominant. Thus a new generic type has been produced by the simple dropping out of one set of characters.

In 1918, Cockerell recognized two females of a second species of Androgynella, A. subrixator, among the bees of the Philippines, but one of the specimens had twelve-, the other thirteen-jointed antennae. He says that he—

should regard these as simple gynandromorphs of Megachile subrixator, which they may be, but for the fact that a similar type (Androgynella detersa Ckll.) is established as a genuine species in Australia. . . . In our bee the antennal character is not constant and there is more reason for considering the form an ordinary gynandromorph. Therefore I give it the same specific name as that of the species from which it appears without doubt to have been derived. . . . Presumably the male of Androgynella subrixator cannot be distinguished from Megachile subrixator.

There are, however, other indications of the occurrence of intersexes or gynandromorphs as normal taxonomic forms among tropical Megachilids. During the past summer, Mr. T. B..Mitchell, who has been working in my laboratory on the bees of the genus Megachile, has discovered among the South American forms not only certain species in which the females have thirteen-jointed antennae and lack the ventral scopa, so that they are most naturally placed in Cockerell's genus Androgynella, but several other species in which the females have the structure of anteroposterior gynandromorphs, the head, thorax, legs, and antennae being male, the abdomen, female. The specimens are so numerous as to preclude their being mere anomalies like the gynandromorphs of other insects taken in the field and to suggest that they may be the normal, albeit intersexual females of their respective species. An account of these singular bees will be published in the near future.

The foregoing discussion of the intersexes is, of course, a mere sketch and fails to do justice to their great importance even in the higher animals and man. But the intersexes are merely a class of a much more comprehensive group of phenomena that are becoming more and more conspicuous in psychological, psychopathological, and sociological, as well as in morphological, physiological, and genetic investigations. I refer to the scissions, or dissociations which so frequently prevent the organism from attaining to complete structural and behavioristic integration and equilibrium. Such dissociations are manifested in the activities of schizophrenics and homosexuals and even in the structural and physiological characters of eunuchoids, pseudohermaphrodites, tetanoid eidetics, etc. Many of these anomalies are clearly cases of intersexuality, as Goldschmidt has shown in a very suggestive paper ('16). And, undoubtedly, the dual, bigametic, and bisexual genetic structure, or genotype of the multicellular organism is responsible both for the so-called 'schizoid' constitutions and the antinomies of character and personality which are so frequently observed in more normal

individuals, as Kretschmer ('25), Hoffmann ('26), Walther Jaensch ('26), and others maintain. As in the case of intercastes and intersexes generally, we are confronted with manifestations of genetic, morphological, and behavioristic characters which are normally latent, but which may be activated by unusual environmental stimuli, such as shock, parasitism, and abnormal nutrition at certain susceptible periods in ontogenetic development.

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